Quaternary herpetofaunas of the British Isles : Taxonomic descriptions,palaeoenvironmental reconstructions, and biostratigraphic implications

Gleed-Owen , Christopher Paul

Award date:
1998

Awarding institution:
Coventry University

QUATERNARY HERPETOFAUNAS OF THE BRITISH ISLES: TAXONOMIC DESCRIPTIONS, PALAEOENVIRONMENTAL RECONSTRUCTIONS, AND BIOSTRATIGRAPHIC IMPLICATIONS

by

Christopher Paul Gleed-Owen

A dissertation submitted in partial fulfilment of the University's requirements for the degree of Doctor of Philosophy

Coventry University

March
1998

To Mum and Dad

Abstract

This project aims to study fossil amphibian and reptile (herpetofaunal) remains from Quaternary sites in the British Isles. This neglected group of vertebrates hold great potential for Quaternary Science. Collectively, they cover a wide range of ecological tolerances, although individual species often have very specific tolerances.

The biology and ecology of individual species are discussed (Chapter 2) to facilitate their use in Quaternary palaeoenvironmental reconstructions, and an account of previous work on fossil herpetofaunas is given (Chapter 3). Very little work on fossil herpetofaunas has been carried out in the British Isles, mainly due to a lack of the required osteological expertise. The preparation and study of a modern osteological collection (Chapter 4), for comparative purposes, has therefore constituted a large and essential part of the project. The resulting manual for the identification of fossil herpetofaunal remains, appropriately illustrated with SEM's and hand-drawn figures, is presented (Chapter 5). The difficulties encountered in identifying some taxa are discussed in detail, and points of caution are stressed where necessary.

The acquired proficiency has been applied to over forty sites, from which herpetofaunal remains are systematically described (Chapter 6). The existing stratigraphic, biotic and archaeological evidence from these sites is considered alongside the new findings, which include the AMS radiocarbon dating of herpetofaunal remains. Palaeoenvironmental, biostratigraphic, zoogeographic and other inferences are discussed, and their place within the existing Quaternary framework for the British Isles is considered (Chapters 7-9). Specific topics relating to the interpretation of fossil herpetofaunas are discussed (Chapter 7), and a synthesis of herpetostratigraphic data and its implications is presented (Chapter 8). The natterjack toad, *Bufo calamita*, has proved especially useful in palaeoenvironmental reconstruction, and particular space is devoted to this species (Chapter 9). Suggestions for future work are set out in the final section.

Quaternary herpetofaunas of the British Isles: taxonomic descriptions, palaeoenvironmental reconstructions, and biostratigraphic implications

Contents

	Page
Contents	i
List of figures	vi
List of tables	xi
1. Introduction	1
1.1 Background	1
1.2 Aims and achievements of the project	1
1.3 The modern British herpetofauna	2
1.4 Other European species considered	4
1.5 Taxonomy	4
1.6 Quaternary chronostratigraphic terminology	7
1.7 Abbreviations used	8
2. Biology, ecology and distribution	9
Class Amphibia	9
Order Caudata	10
Family Salamandridae	10
Salamandra salamandra	10
Triturus marmoratus	12
Triturus cristatus	14
Triturus alpestris	17
Triturus vulgaris	19
Triturus helveticus	22
Order Anura	22
Family Discoglossidae	25
Bombina variegata	25
Bombina bombina	25
Alytes obstetricans	28
Family Pelobatidae	28
Pelobates cultripes	30
Pelobates fuscus	30
Family Pelodytidae	33

Pelodytes punctatus 33
Family Bufonidae 33
Bufo bufo 35
Bufo calamita 35
Bufo viridis 42
Family Hylidae 42
Hyla arborea 42
Hyla meridionalis 45
Family Ranidae 47
Rana temporaria 47
Rana arvalis 50
Rana dalmatina 52
Rana ridibunda 54
Rana lessonae 58
Rana esculenta 60
Class Reptilia 63
Order Chelonia 63

Family Emydidae 63
Emys orbicularis 63

Order Sauria 65
Family Lacertidae 66
Lacerta viridis 66
Lacerta agilis 68
Lacerta vivipara 68
Podarcis muralis 73
Family Anguidae 75
Anguis fragilis 75
Order Ophidia 78
Family Colubridae 78
Coluber viridiflavus 79
Elaphe longissima 79
Natrix natrix 82
Natrix maura 85
Natrix tessellata 85
Coronella austriaca 88
Family Viperidae 91

Vipera berus 91
Vipera aspis 91

3. Literature review and critique of fossil herpetofaunas from the British Isles 96
3.1 Introduction 96
3.2 Early Middle Pleistocene 98
3.3 Late Middle Pleistocene 102
3.4 Late Pleistocene (except Devensian Lateglacial) 109
3.5 Devensian Lateglacial and Holocene 111

4. Methodologies 117
4.1 Existing comparative material studied 117
4.2 Laboratory preparation of comparative material 118
4.3 Study methods 122

5. A manual for the identification of fossil herpetofaunal remains 124
5.1 Introduction 124
5.2 Salamandridae 127
5.3 Anura 153
5.4 Discoglossidae 162
5.5 Pelobatidae 167
5.6 Pelodytidae 169
5.7 Bufonidae 171
5.8 Hylidae 190
5.9 Ranidae 194
5.10 Emydidae 220
5.11 Lacertidae 224
5.12 Anguidae 234
5.13 Ophidia 241

6. New herpetofaunal assemblages studied 255
6.1 Southeast England 257
Sutton Courtenay 257
Cassington 261
Stanton Harcourt 267
Marsworth 277
Ightham Fissures 279
Chislet 282

Boxgrove 284
6.2 Southwest England 290
Kent's Cavern 290
Cow Cave 296
Tornewton Cave 299
Broken Cavern 309
Three Holes Cave 322
Torbryan Six Cave 331
Wookey Hole 332
Milton Hill Cave 337
Denny's Hole 340
Lower Cave 342
Rogers' Cave 343
6.3 Wales 350
Madawg Rockshelter 350
Hoyle's Mouth Cave 353
Little Hoyle Cave 359
Potter's Cave 364
Cathole 368
Pontnewydd Cave 370
6.4 Fens and East Anglia 375
Coveney 376
Deeping St. Nicholas 383
Pinchbeck 389
Market Deeping 390
Gosberton Third Drove 394
Gosberton Mornington House 395
Gosberton Chopdike Drove 397
Terrington St. Clement 404
West Walton 406
Walpole St. Andrew 408
Deeping St. James 409
6.5 Northern England 412
Pin Hole Cave 414
Robin Hood's Cave 417
Whitemoor Channel 420
6.6 Scotland 423
Badger Cave 423

Bone Cave 423
Smoo Cave 435
6.7 Ireland 439
Plunkett Cave 439
Dermot and Grania's Bed Cave 442
Pig Cave 444

7. Taphonomy, dating, ecological and geographical issues - a discussion 446
7.1 Taphonomy of fossil herpetofaunal assemblages 446
7.2 Dispersal and immigration - some ideas and concepts 448
7.3 Locations of glacial refugia 450
7.4 AMS radiocarbon dating of herpetofaunal remains 453
7.5 Age of the Creag nan Uamh 'frog-earth' and its relationship to deposits elsewhere 455
7.6 *Rana temporaria* in Ireland 459
7.7 Exotic frogs in Fenland/East Anglia, and the possible native status of *Rana lessonae* 459

8. Biostratigraphy and palaeoenvironmental significance of British Quaternary herpetofaunas 462
8.1 Early Middle Pleistocene 462
8.2 Late Middle Pleistocene 469
8.3 Late Pleistocene (except Devensian Lateglacial) 473
8.4 Devensian Lateglacial and Holocene 476

9. *Bufo calamita* in the Late Pleistocene and Holocene 490
9.1 Introduction 490
9.2 AMS radiocarbon dating of Lateglacial and early Holocene records 490
9.3 Lateglacial climate and *Bufo calamita* 491
9.4 Holocene records 495
9.5 Implications for land-bridges and colonisation routes 497
9.6 Microsatellite DNA analyses of modern *Bufo calamita* populations 499
9.5 Pioneer status during later Stage 5 and Middle Devensian Stage 3 500

10. Concluding remarks and recommendations for future work 503

Acknowledgements 505
References 506
Appendix 1 - Inventory of skeletal specimens prepared 542

List of figures

Figure 2.1: *S. salamandra* and its distribution. 11
Figure 2.2: *T. marmoratus* and its distribution. 13
Figure 2.3: *T. cristatus* and its distribution. 15
Figure 2.4: Distribution of *T. cristatus* in Britain. 16
Figure 2.5: *T. alpestris* and its distribution. 18
Figure 2.6: *T. vulgaris* and its distribution. 20
Figure 2.7: Distribution of *T. vulgaris* in Britain. 21
Figure 2.8: *T. helveticus* and its distribution. 23
Figure 2.9: Distribution of *T. helveticus* in Britain. 24
Figure 2.10: *B. variegata* and its distribution. 26
Figure 2.11: *B. bombina* and its distribution. 27
Figure 2.12: *A. obstetricans* and its distribution. 29
Figure 2.13: *P. cultripes* and its distribution. 31
Figure 2.14: *P. fuscus* and its distribution. 32
Figure 2.15: *P. punctatus* and its distribution. 34
Figure 2.16: *B. bufo* and its distribution. 36
Figure 2.17: Distribution of *B. bufo* in Britain. 37
Figure 2.18: *B. calamita* and its distribution. 39
Figure 2.19: Distribution of *B. calamita* in Britain. 40
Figure 2.20: *B. viridis* and its distribution. 43
Figure 2.21: *H. arborea* and its distribution. 44
Figure 2.22: *H. meridionalis* and its distribution. 46
Figure 2.23: *R. temporaria* and its European distribution. 48
Figure 2.24: Distribution of *R. temporaria* in Britain. 49
Figure 2.25: *R. arvalis* and its distribution. 51
Figure 2.26: *R. dalmatina* and its distribution. 53
Figure 2.27: *R. ridibunda* and its distribution. 55
Figure 2.28: Distribution of *R. ridibunda* in Britain (introduced). 56
Figure 2.29: *R. lessonae* and its distribution. 59
Figure 2.30: *R. esculenta* and its distribution. 61
Figure 2.31: *E. orbicularis* and its distribution. 64
Figure 2.32: *L. viridis* and its distribution. 67
Figure 2.33: *L. agilis* and its distribution. 69
Figure 2.34: Distribution of *L. agilis* in Britain. 70
Figure 2.35: *L. vivipara* and its European distribution. 71
Figure 2.36: Distribution of *L. vivipara* in Britain. 72

Figure 2.37: *P. muralis* and its distribution. 74
Figure 2.38: *A. fragilis* and its distribution. 76
Figure 2.39: Distribution of *A. fragilis* in Britain. 77
Figure 2.40: *C. viridiflavus* and its distribution. 80
Figure 2.41: *E. longissima* and its distribution. 81
Figure 2.42: *N. natrix* and its distribution. 83
Figure 2.43: Distribution of *N. natrix* in Britain. 84
Figure 2.44: *N. maura* and its distribution. 86
Figure 2.45: *N. tessellata* and its distribution. 87
Figure 2.46: *C. austriaca* and its distribution. 89
Figure 2.47: Distribution of *C. austriaca* in Britain. 90
Figure 2.48: *V. berus* and its distribution. 92
Figure 2.49: Distribution of *V. berus* in Britain. 93
Figure 2.50: *V. aspis* and its distribution. 95
Figure 3.1: Locations of sites with published herpetofaunal assemblages. 97
Figure 3.2: Herpetofaunal remains from West Runton Freshwater Bed, Norfolk. 99
Figure 3.3: Anuran remains from West Runton Freshwater Bed, Norfolk. 99
Figure 3.4: Herpetofaunal remains from Boxgrove, West Sussex. 101
Figure 3.5: Herpetofaunal remains from Westbury Cave, Somerset. 101
Figure 3.6: Herpetofaunal remains from Cudmore Grove, Essex. 104
Figure 3.7: Herpetofaunal remains from Selsey, West Sussex. 107
Figure 3.8: Reptile remains from Shropham, Norfolk. 107
Figure 3.9: Herpetofaunal rremains from Itteringham, Norfolk. 108
Figure 3.10: *E. orbicularis* remains from Mundesley, Norfolk. 110
Figure 3.11: Herpetofaunal remains from Ightham Fissures, Kent. 113
Figure 3.12: *B. bufo* remains from Whitemoor Channel, Cheshire. 113
Figure 5.1: Newt skulls. 130
Figure 5.2: Salamandrid parasphenoids (ventral view). 131
Figure 5.3 : Salamandrid parasphenoids (dorsal view). 132
Figure 5.4: Salamandrid parietals. 134
Figure 5.5: Salamandrid frontals. 135
Figure 5.6: Salamandrid orbitosphenoids. 136
Figure 5.7: Salamandrid left prootic-exoccipitals. 138
Figure 5.8: Salamandrid premaxillae. 139
Figure 5.9: Salamandrid trunk vertebrae (left lateral view). 141
Figure 5.10: Salamandrid trunk vertebrae (ventral view). 142
Figure 5.11: Salamandrid trunk vertebrae (anterior view). 143
Figure 5.12: Salamandrid trunk vertebrae (dorsal view). 144

Figure 5.13: Salamandrid trunk vertebrae (posterior view). 145
Figure 5.14: Salamandrid caudal vertebrae (left lateral view). 147
Figure 5.15: Salamandrid caudal vertebrae (anterior view). 148
Figure 5.16: Salamandrid right scapulocoracoids. 150
Figure 5.17: *S. salamandra* appendicular skeleton. 151
Figure 5.18: Typical anuran skeleton (*B. bufo*). 154
Figure 5.19: Anuran frontoparietals. 155
Figure 5.20: Anuran sphenethmoids. 156
Figure 5.21: Anuran sacra. 157
Figure 5.22: *R. esculenta* right forelimb and pectoral girdle. 158
Figure 5.23: Anuran left ilia. 159
Figure 5.24: Anuran left ilia (junctura ilioischiadica). 160
Figure 5.25: *R. esculenta* hindlimb. 161
Figure 5.26: *B. bombina* vertebral variation. 164
Figure 5.27: *Bufo* second and third vertebrae. 176
Figure 5.28: *Bufo* sacra and left scapulae. 177
Figure 5.29: *B. bufo* and *B. calamita* ilia. 180
Figure 5.30: *B. calamita* and *B. viridis* ilia. 181
Figure 5.31: Spanish *B. calamita* right ilium, sacrum, left scapula, cranial bones. 182
Figure 5.32: Fossil *B. viridis* left ilia from Ghar Dalam Cave, Malta. 183
Figure 5.33: *H. arborea* left and right ilia, sacrum, left scapula, trunk vertebrae. 191
Figure 5.34: *H. meridionalis* left and right ilia. 192
Figure 5.35: *Rana* third trunk vertebrae. 200
Figure 5.36: *Rana* sacra. 201
Figure 5.37: *Rana* omosternums. 203
Figure 5.38: *R. temporaria* left ilia. 205
Figure 5.39: *R. arvalis* left ilia. 206
Figure 5.40: *R. ridibunda* left ilia. 207
Figure 5.41: *R. lessonae* left ilia and green frog scapulae. 208
Figure 5.42: *R. esculenta* left ilia. 209
Figure 5.43: *R. ridibunda* left ilium. 210
Figure 5.44: *R. lessonae* left ilium. 211
Figure 5.45: *R. esculenta* left ilium. 212
Figure 5.46: *R. dalmatina* left ilium, *R. arvalis* metacarpal, *R. dalmatina* metacarpal. 213
Figure 5.47: *Rana* juncturae ilioischiadicae. 214
Figure 5.48: Green frog urostyles. 217
Figure 5.49: *E. orbicularis* carapace and plastron. 222
Figure 5.50: Lacertid cranium (*L. viridis*) and tail (*L. vivipara* and *P. muralis*). 225

Figure 5.51: Lacertid and anguid trunk vertebrae (dorsal and ventral views). 227
Figure 5.52: Lacertid and anguid trunk vertebrae (anterior and posterior views). 228
Figure 5.53: Lacertid and anguid trunk and caudal vertebrae (left lateral views). 229
Figure 5.54: *L. viridis* vertebrae. 230
Figure 5.55: *A. fragilis* parietal, osteoderms, cervical and other vertebrae. 236
Figure 5.56: *A. fragilis* caudal vertebrae and pelvic girdle. 238
Figure 5.57: Typical colubrid snake skeleton and vertebral nomenclature. 242
Figure 5.58: Snake trunk vertebrae (dorsal view). 244
Figure 5.59: Snake trunk vertebrae (ventral view). 245
Figure 5.60: Snake trunk vertebrae (anterior view). 246
Figure 5.61: Snake trunk vertebrae (posterior view). 247
Figure 5.62: Snake trunk vertebrae (left lateral view). 248
Figure 5.63: *C. viridiflavus* mid-trunk, cervical and caudal vertebrae. 249
Figure 5.64: *E. longissima* mid-trunk, cervical and caudal vertebrae. 250
Figure 5.65: *V. aspis* mid-trunk, cervical and caudal vertebrae. 251
Figure 6.1: Location and lithostratigraphy at Cassington, Oxfordshire. 262
Figure 6.2: Amphibian remains from Cassington, Oxfordshire. 264
Figure 6.3: Plan and lithostratigraphy at Stanton Harcourt, Oxfordshire. 268
Figure 6.4: Amphibian remains from Stanton Harcourt, Oxfordshire. 271
Figure 6.5: Anuran remains from Stanton Harcourt, Oxfordshire. 272
Figure 6.6: Anuran remains from Stanton Harcourt, Oxfordshire. 274
Figure 6.7: Anuran remains from Hyaena Stratum, Tornewton Cave, Devon. 274
Figure 6.8: Location and sections through deposits at Marsworth, Buckinghamshire. 277
Figure 6.9: *B. calamita* ilia from Ightham Fissures, Kent. 279
Figure 6.10: *B. calamita* ilia from Ightham Fissures, Kent. 280
Figure 6.11: Location and lithostratigraphy at Boxgrove, West Sussex. 284
Figure 6.12: Survey and schematic sections at Kent's Cavern, Devon. 291
Figure 6.13: Herpetofaunal remains from Wolf's Den, Kent's Cavern, Devon. 294
Figure 6.14: *B. calamita* ilia from Cow Cave, Devon 298
Figure 6.15: Location of Torbryan Caves and lithostratigraphy of Tornewton Cave, Devon. 300
Figure 6.16: *B. calamita* remains from Tornewton Cave (Devon), Wookey Hole (Somerset) and Sutton Courtenay (Oxfordshire). 303
Figure 6.17: Herpetofaunal remains from Hyaena Stratum, Tornewton Cave, Devon. 304
Figure 6.18: Stratigraphy of Tornewton Cave, Three Holes Cave and Broken Cavern, Devon. 308
Figure 6.19: Lithostratigraphic section of deposits at Broken Cavern, Devon. 310
Figure 6.20: Anuran remains from Three Holes Cave and Broken Cavern, Devon. 315
Figure 6.21: Herpetofaunal remains from Three Holes Cave and Broken Cavern, Devon. 316
Figure 6.22: Lithostratigraphy at Three Holes Cave and Torbryan Six Cave, Devon. 323

Figure 6.23: Stratigraphy at Wookey Hole Hyaena Den and Denny's Hole, Somerset. 333
Figure 6.24: Anuran remains from Rogers' Cave (Herefordshire), Milton Hill Cave (Somerset), and Denny's Hole (Somerset). 338
Figure 6.25: Location of Wye Valley Caves, Herefordshire and Gwent. 344
Figure 6.26: Plan and lithostratigraphy of Rogers' Cave, Herefordshire. 345
Figure 6.27: Plan and lithostratigraphy of Madawg Rockshelter, Gwent. 351
Figure 6.28: Locations of the South Wales caves, and survey of Hoyle's Mouth Cave, Dyfed. 354
Figure 6.29: Plan and lithostratigraphy of Little Hoyle Cave, Dyfed. 360
Figure 6.30: Schematic section through Little Hoyle Cave, Dyfed. 361
Figure 6.31: Plan and sections at Potter's Cave (Dyfed) and lithostratigraphy at Cathole (West Glamorgan). 364
Figure 6.32: Location, lithostratigraphy and survey of Pontnewydd Cave, Clwyd. 370
Figure 6.34: Herpetofaunal remains from Coveney, Cambridgeshire. 379
Figure 6.33: Location and plan of Bronze Age barrow at Deeping St. Nicholas, Lincolnshire. 384
Figure 6.35: Anuran remains from Whitemoor Channel (Cheshire), Deeping St. Nicholas (Lincolnshire), Gosberton (Lincolnshire) and Terrington St. Clement (Norfolk). 386
Figure 6.36: Right ilium of *R. lessonae* from Gosberton Chopdike Drove, Lincolnshire. 402
Figure 6.37: Location and schematic section at Deeping St. James, Lincolnshire. 410
Figure 6.38: Plan of Creswell Caves, and lithostratigraphy at Pin Hole Cave, Derbyshire. 413
Figure 6.39: Plan and lithostratigraphy at Robin Hood's Cave, Derbyshire. 418
Figure 6.40: Location, survey and sections through Whitemoor Channel, Cheshire. 421
Figure 6.41: Location and survey of Creag nan Uamh Caves, Highland Region. 424
Figure 6.42: Schematic lithostratigraphies of Creag nan Uamh Caves, Highland Region. 425
Figure 6.43: Amphibian remains from Badger Cave and Bone Cave, Creag nan Uamh. 428
Figure 6.44: *R. temporaria* remains from Bone Cave, Creag nan Uamh. 429
Figure 6.45: Reptile remains from Badger Cave and Bone Cave, Creag nan Uamh. 431
Figure 6.46: Plan of Smoo Cave, Highland Region, and section through its midden. 433
Figure 6.47: Schematic lithostratigraphy at Smoo Cave, Highland Region. 434
Figure 6.48: Plan and sections at Coffey Cave (near Plunkett Cave), Co. Sligo. 438
Figure 8.1 Locations of sites with herpetofaunal data used in Table 8.1. 464
Figure 9.1: *B. calamita* bones submitted for AMS radiocarbon dating. 488

List of tables

Table 1.1: Taxonomy of herpetofaunal species considered. 5
Table 6.1: Herpetofaunal taxa recovered from each sample at Stanton Harcourt. 269
Table 6.2: Herpetofaunal taxa recovered from each sample at Kent's Cavern. 292
Table 6.3: Herpetofaunal taxa recovered from each sample of Hyaena Stratum, Tornewton Cave. 302
Table 6.4: Herpetofaunal taxa recovered from each sample at Broken Cavern. 312
Table 6.5: Herpetofaunal taxa recovered from each sample at Three Holes Cave. 324
Table 6.6: Herpetofaunal taxa recovered from each sample of Wooky Hole Hyaena Den. 332
Table 6.7: Herpetofaunal taxa recovered from each sample at Rogers' Cave. 346
Table 6.8: Herpetofaunal taxa recovered from each sample at Madawg Rockshelter. 350
Table 6.9: Herpetofaunal taxa recovered from each sample at Hoyle's Mouth Cave. 355
Table 6.10: Stratigraphic relationships between evidence from Little Hoyle Cave. 361
Table 6.11: Herpetofaunal taxa recovered from each sample at Little Hoyle Cave. 362
Table 6.12: Herpetofaunal taxa recovered from each sample at Potter's Cave. 363
Table 6.13: Herpetofaunal taxa recovered from each sample at Pontnewydd Cave. 372
Table 6.14: Herpetofaunal taxa recovered from each sample at Coveney. 377
Table 6.15: Herpetofaunal taxa recovered from each sample at Deeping St. Nicholas. 385
Table 6.16: Herpetofaunal taxa recovered from each sample at Pinchbeck. 389
Table 6.17: Herpetofaunal taxa recovered from each sample at Market Deeping. 390
Table 6.18: Herpetofaunal taxa recovered from each sample at Gosberton Third Drove. 394
Table 6.19: Herpetofaunal taxa recovered from each sample at Gosberton Mornington House. 395
Table 6.20: Herpetofaunal taxa recovered from each sample at Gosberton Chopdike Drove. 397
Table 6.21: Herpetofaunal taxa recovered from each sample at Terrington St. Clement. 404
Table 6.22: Herpetofaunal taxa recovered from each sample at West Walton. 406
Table 6.23: Herpetofaunal taxa recovered from each sample at Walpole St. Andrew. 408
Table 6.24: Herpetofaunal taxa recovered from each sample at Deeping St. James. 409
Table 6.25: Herpetofaunal taxa recovered from each sample at Pin Hole Cave. 415
Table 6.26: Herpetofaunal taxa recovered from each sample at Robin Hood's Cave. 419
Table 6.27: Herpetofaunal taxa recovered from each sample at Bone Cave and Badger Cave. 426
Table 6.28: Herpetofaunal taxa recovered from each sample of Smoo Cave midden. 437
Table 7.1: Probable locations of glacial refugia. 450
Table 7.2: AMS radiocarbon dates on herpetofaunal remains from Creag nan Uamh. 454
Table 8.1: Fossil occurrences of herpetofaunal taxa from Quaternary of British Isles. 463
Table 8.2: Lateglacial and Holocene herpetostratigraphy of the British Isles. 477
Table 9.1: AMS radiocarbon dates on *B. calamita*, with calibrated ages. 489

1 Introduction

1.1 Background

Amphibians and reptiles are widely distributed in Europe, ranging in latitude from the high arctic to the Mediterranean Sea. Some taxa occur throughout most of this latitudinal range but most have more restricted distributions. Collectively they have a wide range of ecological and climatic tolerances, but individual species are generally rather particular. They are recognised, as a group, as being very sensitive to environmental change, whether this be alteration in habitat, climate or other factors (e.g. Corbet, 1989). Ecological requirements vary between species and influence their distribution, abundance and the continuity of their range. Some species are limited by seasonal conditions such as a minimum summer temperature needed for breeding to be successful. The longitudinal distribution of some taxa demonstrates their association with either oceanic or continental type climates. Often, parameters such as these are combined with others such as the need for suitable habitats or a lack of competition. Amphibians, in particular, are restricted to moister areas, and to places with suitable water bodies for breeding. Reptiles often require dry, exposed areas in which to bask, and protected places, often where moisture and temperature is regulated, to deposit their eggs. Amphibian and reptile species can be fast colonisers of suitable terrain, some species being adept at exploiting newly-created or changing environments. Amphibian population dynamics are characterised by dramatic fluctuations, with high mortality rates, particularly during immaturity. They are good indicators of certain environmental conditions, such as the proximity of shallow pools of a particular nature. Some taxa are more fastidious than others, and allow the inference of specific environmental conditions. Thus the interpretation of fossil herpetofaunal remains, can provide valuable information regarding the paleoenvironment of the locality in which the animals were living, as well as more regional conditions. Hence, this group of vertebrates has considerable potential for palaeoenvironmental reconstruction in the Quaternary.

Amphibian and reptile species in Europe mostly have long-lived ancestries, often with fossil records extending well back into the Tertiary. The same species that were living throughout the Pleistocene are still alive today. Unlike many mammal species which have become extinct or have evolved over the same timescale, herpetofaunal remains from Quaternary deposits are readily useable for inferring palaeoenvironments. However, Quaternary palaeoherpetology has been little studied in the British Isles. In comparison with other branches of plant and animal palaeontology, not much is known about the Quaternary history of amphibians and reptiles in the British Isles. Thus, an unknown and probably large quantity of palaeoenvironmental and biostratigraphic information has hitherto been left unexploited. This situation has been propagated by the lack of any workers in Britain with the expertise to identify amphibian and reptile remains.

1.2 Aims and achievements of the project

The aim of the current project has been to address the deficiency in palaeoherpetological expertise in Britain. Obviously, the timescale available for a doctorate thesis is not enough to 'catch up' with other branches of Quaternary palaeontology, but a fair degree of advancement has been achieved here. The primary aim of the project has been the development of palaeoherpetology as a technique. This has involved a comprehensive programme of modern comparative osteological research, in order to assist the study of fossil material. Identification keys do not exist for amphibian and reptile remains, and the continental literature on osteology and identification criteria is widely dispersed and, even when compiled together, it is far from comprehensive. Useful herpetological type collections do not exist in Britain. It has therefore been necessary to build one. A collection of 125 skeletons has been gathered and prepared, with the acknowledged help of many people. Some species have not been obtained, but visits to collections in Madrid and Kraców, and material borrowed from Prague have enabled study of those species not collected yet.

Detailed study has allowed the development of identification criteria for many species. To achieve maximum benefit, this knowledge should be transferrable to other workers wishing to study herpetofaunal remains via descriptions, SEM micrographs and drawings. Thus an attempt at developing an identification manual for fossil amphibian and reptile remains is presented (Chapter 5). Application of this knowledge has been the next stage. The diagnostic criteria derived from detailed osteological studies have been applied to a large number of sites with fossil remains from the British Isles. A sizeable volume of fossil herpetofaunal remains has been identified, and these are presented systematically in Chapter 6. Most of the material which has become available derives from Devensian Lateglacial and Holocene sites, hence the emphasis has been on this latest part of the Quaternary. This is clearly not an exhaustive study of British Quaternary herpetofaunas, but by synthesising the new and existing data, it provides a satisfactory overview, upon which future work can be founded. The data provide the basis for deriving a substantial amount of palaeoenvironmental, biostratigraphic and biogeographic information, and the allows construction of the beginnings of a biostratigraphic framework (Chapters 8 and 9).

At the close of this project, a worthy comparison can be drawn with the sentiments of D. Bramwell who in 1960 was in a similar position, involved in the task of learning to identify British bird fossils:

> '... bird-remains are much less well known than the contemporary mammals. ... There are great difficulties in correctly naming certain bones, due to the very slight variations between members of the same genus .... the collecting of reference material has been a big task ...' (Bramwell, 1960)

1.3 The modern British herpetofauna

The British Isles are defined here as England, Scotland, Wales and Ireland, and do not include the Channel Islands. Britain is defined as England, Scotland and Wales, and Ireland refers to the

whole island of Ireland. The present herpetofauna of the British Isles consists of twelve species accepted as native (Arnold, 1995). The range and distribution of the British species varies considerably and the most comprehensive records published are those produced by the Institute of Terrestrial Ecology, Monks Wood, Cambridgeshire (Arnold, 1973, 1995). Arnold (1973) produced maps with coverage of the entire British Isles; Arnold (1995) gave updated and more reliable records for Britain only. These distribution maps are reproduced in the respective sections of Chapter 3. It is recognised that surveying for the maps has not been continuous over some parts of the British Isles, particularly areas of low human population density, but the overall ranges are not affected and distributions are comparable between species. Distribution maps, showing by a dot, species presence in an area, do not reflect its relative abundance therein, neither do they detail the relevant habitat(s).

The three newts, two toads and a frog, three lizards and three snakes exploit a very wide range of habitats with great differences in their geographical ranges and abundance. *Triturus cristatus* (great crested or warty newt), *Triturus vulgaris* (smooth or common newt) and *Triturus helveticus* (palmate newt) represent the Salamandridae in Great Britain, with only *T. vulgaris* being present in Ireland. Of the two toads, *Bufo bufo* (Eurasian common toad) is widespread in Britain but absent from Ireland, but *Bufo calamita* (natterjack toad) has a restricted distribution in both Britain and Ireland. *Rana temporaria* (Eurasian common frog) is present throughout Britain and Ireland. *Lacerta vivipara* (common lizard) is widespread in Britain and most of Ireland, but *Lacerta agilis* (sand lizard) is restricted in Britain and absent from Ireland. *Anguis fragilis* (slow-worm) is a legless lizard widely distributed throughout Britain, but absent from Ireland. *Vipera berus* (adder or viper) is widespread throughout Britain, but is not found in Ireland. *Natrix natrix* (grass snake) is found throughout most of England, Wales and southern parts of Scotland, but is absent from Ireland. *Coronella austriaca* (smooth snake) is restricted to a small area of southern Britain and is also absent from Ireland.

All twelve species can be locally abundant, but are controlled to varying degrees by habitat availability. Three (*B. calamita, L. agilis* and *C. austriaca*) are much less widely distributed and abundant than the other nine. The rarer species are more strictly protected by British and European law. The Wildlife and Countryside Act (1981 and later amendments) covers all twelve species in Britain, and its Schedule 5 offers maximum protection to *T. cristatus, B. calamita, L. agilis* and *C. austriaca*. The Bern Convention (on Conservation of European Wildlife and Natural Habitats), particularly Appendix II, and EC Directive 92/43/EEC of 21 May 1992, particularly Annex IVa, offer maximum protection to the same species. Though there have been attempts to explain the restricted distributions of the rarer species, no agreement has been reached. It is hoped that the examination and interpretation of fossil material in this thesis will contribute to this debate and to other issues concerning the modern ecology of the British herpetofauna.

1.4 Other European species considered

In addition to the twelve species known to be native to Britain, consideration has been given to 25 currently exotic species. Some of these have been recorded fossil from British Quaternary sites. The others have been selected because their northern limit today is at or above the northern limit of the most southerly species yet recorded from the British Pleistocene, *H. meridionalis* (recorded from Itteringham: Holman, 1992b). The northern limit of *H. meridionalis* is uncertain (García París, 1997), but a line of latitude somewhere between the mouths of the Gironde and Loire rivers seems most appropriate. This line is therefore taken to represent the southern limit of the herpetofaunal 'catchment area' from which immigration to the British Isles is likely to have taken place. The distribution maps provided by Gasc *et al* (1997) have been used to represent modern geographical ranges. Many of the twenty-five species reach the continental coasts of the English Channel and North Sea, and some (e.g. *Rana arvalis*) extend considerably further north than this, in Fennoscandia and Russia. Only one species (*Triturus montandoni*) with a distribution north of the catchment latitude has not been included. *T. montandoni* is endemic to the Carpathian and Tatra Mountains (Gasc *et al*, 1997; Necas *et al*, 1997), and is unlikely to have reached Britain during the Pleistocene. The ocellated lizard *Lacerta lepida* of southwest Europe almost reaches the catchment latitude but has not been included here.

For some of the currently exotic species (e.g. *Triturus alpestris, Alytes obstetricans, Hyla arborea, Rana ridibunda* and *Rana esculenta*), introduced populations are already present and persistent in Britain (Arnold, 1995). These species are clearly suited to the present climate and their natural occurrence must have been prevented (or arrested) by other factors such as geographical isolation. A few populations of *R. esculenta* and *R. lessonae* cannot be traced to introductions and may in fact be native (Snell, 1994; Arnold, 1995). Virtually all 37 of the species considered here equate with the herpetofauna of the European region demarcated as the 'Northwest zone' defined by Martínez Rica (1997). This climatic zone has a strong oceanic influence. It is typified by warm summers and has no months with a mean temperature below 0°C. It includes the British Isles and stretches from France to South Norway, with 22 species of amphibian and 15 of reptile. *T. helveticus* is considered a representative species (Martínez Rica, 1997). Effectively, this region is the same as that considered here to be the potential Pleistocene catchment for immigrations to the British Isles. The repeated climatic oscillations of the Pleistocene would not have been favourable to herpetofaunas (Rage, 1997), but only one family, the Palaeobatrachidae, appears to have become extinct during this time (Sanchiz and Szyndlar, 1984; Rage, 1997).

1.5 Taxonomy

A total of thirty-seven species, from twelve families, have been studied in the current project. The system of taxonomic nomenclature used throughout follows the International Code of Zoological Nomenclature, described by Frost (1985). The families, genera and species are discussed in the

same order throughout, following the sequence used by Arnold and Burton (1978). Table 1.1 shows, in hierarchical order, the taxonomic positions of the species studied. Original authors are given in the relevant species sections in Chapter 3, along with the most commonly used vernacular names in the English language.

Table 1.1

Class	Amphibia
Order	Caudata
Suborder	Salamandroidea
Family	Salamandridae
	Salamandra salamandra
	Triturus marmoratus
	Triturus cristatus
	Triturus alpestris
	Triturus vulgaris
	Triturus helveticus
Order	Anura
Family	Discoglossidae
	Bombina variegata
	Bombina bombina
	Alytes obstetricans
Family	Pelobatidae
Subfamily	Pelobatinae
	Pelobates cultripes
	Pelobates fuscus
Family	Pelodytidae
	Pelodytes punctatus
Family	Bufonidae
	Bufo bufo
	Bufo calamita
	Bufo viridis
Family	Hylidae
	Hyla arborea
	Hyla meridionalis
Family	Ranidae
Subfamily	Raninae
	Rana temporaria

	Rana arvalis
	Rana dalmatina
	Rana ridibunda
	Rana lessonae
	Rana esculenta
Class	Reptilia
Order	Chelonia
Family	Emydidae
Subfamily	Emydinae
	Emys orbicularis
Superorder	Squamata
Order	Sauria
Suborder	Lacertilia
Family	Lacertidae
	Lacerta viridis
	Lacerta agilis
	Lacerta vivipara
	Podarcis muralis
Family	Anguidae
Subfamily	Anguinae
	Anguis fragilis
Order	Serpentes
Suborder	Alethinophidia
Superfamily	Colubroidea
Family	Colubridae
	Coluber viridiflavus
	Elaphe longissima
	Natrix natrix
	Natrix maura
	Natrix tessellata
	Coronella austriaca
Family	Viperidae
Subfamily	Viperinae
	Vipera berus
	Vipera aspis

1.6 Quaternary chronostratigraphic terminology

The stratigraphic terminology used for chronological divisions of the Quaternary has often been at least unclear and sometimes ambiguous or misleading. Here, the term 'Quaternary' will be used to describe the chronological period which is constituted by the Pleistocene and the Holocene epochs. The Pleistocene is used to describe all but the last ten thousand years of the Quaternary, which timespan encompasses the Holocene, i.e. up to the end of the last period of glaciation and periglaciation in the British Isles. Pleistocene episodes of largely 'cold' climate in the British Isles, characterised by terrestrial glacial and periglacial deposits and low sea levels, will be referred to as cold stages. In contrast, periods characterised by a temperate climate, with sufficient warmth to support a thermophilous flora and fauna, predominantly organic deposits and high sea levels, will be referred to as interglacials. Shorter periods of temperate climate, recognised within a cold stage, will be described as interstadials.

As the dating and correlation of these events at different terrestrial sites is problematic, agreement on the terminology of the stages recognised is correspondingly difficult to reach. Probably the best and most widely used current system of correlation is by comparison with the deep-ocean Oxygen Isotope (O.I.) record, such as that described by Shackleton and Opdyke (1973, 1976). Isotopic composition curves such as this have been accepted as the most reliable indication of global climatic change over the Quaternary, and have thus been widely used as a standard upon which to base terrestrial correlations. In the British Isles, the terrestrial deposits found so far are insufficiently diagnostic and complete to produce a firm chronological framework which can be correlated with the temperate and cold stages shown by the oceanic record. The evidence is inconsistent in both quantity and quality. Nevertheless, in many cases direct lithostratigraphy and biostratigraphy, together with absolute and relative dating, have allowed a site to be assigned a reasonably firm stratigraphic position within the British record and its tentative correlation with the oxygen isotope record. Also, in recent years, there has been substantial reappraisal of the terrestrial evidence, resulting in the notion that some traditional biostratigraphic correlations (particularly those based on palynological evidence) may be incorrect (Jones and Keen, 1993). Thus, the use of orthodox stage names *sensu* Mitchell *et al* (1973) may in some cases be inappropriate.Thus, provided that workers are consistent in their usage of the O.I. system, this is at present, probably our best means of correlating terrestrial records with global climatic events during the Quaternary. For example, it is widely accepted that the thermal maximum of the Ipswichian/last interglacial in the British Isles and its Eemian equivalent in Europep represents Oxygen Isotope Substage 5e.

A note of caution should be added, however. As the O.I. record is a measure of global ice volumes, rather than an accurate 'palaeothermometer', it should only be treated as such. The O.I. Record (Shackleton and Opdyke, 1976) demonstrates that Stage 7 has two peaks, and Stages 9, 11, 13 and 15 are each made up of a number of peaks. As the heights and shapes of these peaks vary between cores V28-238 and V28-239 and other cores (e.g Bassinot *et al*, 1994), the curves

probably hide the full range of climatic fluctuations, which in reality were probably much more complex and erratic. The complexity of fluctuations within the last 120,000 years demonstrated in the ice-core and deep-ocean records (Grootes *et al*, 1993; Bender *et al*, 1994; Adkins *et al*, 1997), suggests that earlier events might have been equally complex. Current trends in chronostratigraphic correlation tend to assume that one interglacial equals one Stage on the O.I. curve. Unless there is substantial sedimentological and biostratiographic evidence to support this, it may be too simplistic. Two distinct biostratigraphic units might relate to two separate peaks of the same Stage. For example, in Stage 7, a more thermophilous fauna appears to have been present in Britain during Substage 7c, and a less thermophilous fauna was present during Substage 7a (Schreve, 1998).

In the following text, terrestrial deposits in the British Isles will be referred to by their assumed equivalent O.I. Stage Number. For ease of use, this will be shortened to, for example, 'Stage 7' for the interglacial believed to precede the Ipswichian. In some cases, it is still considered acceptable to use stage names, based largely on lithostratigraphical and biostratigraphical evidence. Thus, where appropriate, stage names such as the Ipswichian will be used here. As there is uncertainty over the correlation and age of some sites with existing named stages, stage names will be placed in inverted commas when such a situation occurs.

There does not appear to be a formal definition for distinction between the terms fossil and subfossil. When describing bone assemblages here, the term 'fossil' has almost always been used. Yet in some situations, such as the study of bones from sediments of historical age, this term does not seem appropriate, and the term 'subfossil' has been used.

1.7 Abbreviations

The following abbreviations are used in the text, when referring to institutional and private collections:

BM	British Museum (Quaternary Section, Franks House), London
CC	Creswell Crags Visitor Centre collection, Derbyshire
CGO	Chris Gleed-Owen private collection (at COV)
COV	Coventry University (Centre for Quaternary Science), West Midlands
CM	Cromer Museum, Norfolk
JC	John Clayden private collection, East Runton, Norfolk
MNCN	Museo Nacional de Ciencias Naturales, Madrid
NCM	Norwich Castle Museum, Norfolk
NHM	Natural History Museum (Department of Palaeontology), London
NMW	National Museum of Wales (Department of Archaeology), Cardiff
ZZSid	Z. Szyndlar collection (at PAS)
PAS	Polish Academy of Science, Kraków
ZR	Zbynek Rocek collection, Department of Paleontology, Academy of Sciences, Prague

2 Biology, ecology and distribution

Introduction

Twenty-three amphibian and fourteen reptile species are considered, because of their presence in the British Isles today, their fossil occurrence, or their likelihood as Pleistocene immigrants. Each species is discussed with respect to its taxonomy, morphology, biology, physiology, ecology, modern distibution and fossil records. Each species account attempts to include any information which may be relevant to its use in palaeoenvironmental reconstruction. It is assumed that the ecological tolerances of the species have remained unchanged throughout the Quaternary, and that palaeoenvironmental inferences can be drawn from this information.

Osteological evidence indicates that amphibian and reptile species have remained largely unchanged for a long time period (Sanchiz and Mlynarski, 1979). Some living species have records extending back well into the Tertiary. Existing British fossil records for each species are given for ease of reference. Some of the species have continental fossil records pre-dating the Pleistocene, but no living species have British fossil occurrences older than the Middle Pleistocene.

Distribution maps are taken from Gasc *et al* (1997). These vary considerably from, and supersede, those given by Arnold and Burton (1978). Solid dots refer to records since 1970, open circles are records before 1970, crosses are records now extinct, and triangles are known introductions.

Class: **Amphibia** Linnaeus 1758

There are three living orders: the Caudata or Urodela (salamanders and newts); the Anura (frogs and toads); and the Gymnophiona or Apoda (caecilians - limbless subterranean amphibians which remain relatively unstudied). Amphibians are ectothermic vertebrates, normally with two pairs of limbs, and glandular skin (Duellman and Trueb, 1986). A suitable body of water is essential for amphibian reproduction. This must persist for long enough to allow metamorphosis of the young animals before the following winter, though overwintering in water is known. Temperature is a key factor in controlling amphibian reproduction, and is a direct control over the success of reproducion. Some species require warmer ambient temperatures than others, which not only controls the timing of reproduction but also the geographical limits for its success. The amphibian life cycle usually involves the deposition of jelly-like eggs in water. The young develop as free swimming larvae which grow limbs, eventually metamorphose and move onto land. Some species are almost totally aquatic, whilst others are almost entirely terrestrial. Mortality is typically very high throughout the various growth stages in an amphibian's life. Fish, other vertebrates and many invertebrates such as dragonfly larvae feed on amphibian eggs and larvae. Cannibalism between and within species is also commonplace. Carnivorous mammals, particularly mustelids, herons and large fish probably account for most predation of adults. The larvae of many amphibians also

feed on the eggs and larvae of other species. Of the European species of amphibian, six urodeles and seventeen anurans are considered here.

Order: Caudata Oppel 1811

Suborder: Salamandroidea Noble 1931

Family: Salamandridae Gray 1825

The order Caudata (or Urodela) represents all tailed amphibians and contains the family Salamandridae, the newts and salamanders. They generally have smooth velvety skin, which is moist whilst on land. Unlike anurans, they possess moveable heads. Most have legs and during their terrestrial stages, often move over wide areas, foraging and between refugia and breeding pools. The newts are generally more aquatic than the salamanders of Europe. The phylogeny of the fossil caudata has been under-studied. Fifty-six genera have been described, of which twenty-five are extant (Estes, 1981). Almost all of the European caudata, including the six species considered here, belong to the family Salamandridae. One species belongs to the genus *Salamandra*, the other five belong to the genus *Triturus*.

Salamandra salamandra (Linnaues 1758) **Fire salamander**

A robust, very terrestrial, relatively short-tailed salamander, attaining lengths up to 280mm, but more commonly less than 200mm (Arnold and Burton, 1978). The body is mainly black, but with a covering of intensely coloured markings, ranging from yellow to orange, and forming a variety of patterns including irregular stripes. Like many other amphibians, its large paratoid glands, located on either side of the head behind the eyes, produce a secretion which acts as a deterrent to predators. It is strongly adapted to forested areas, mainly deciduous but sometimes coniferous (Veith, 1997), and is associated typically with damp montane environments, reaching up to altitudes of 2,000m in the southern parts of its range (Arnold and Burton, 1978). Despite this association, *S. salamandra* may also survive for long periods in deforested regions, e.g. around the Mediterranean Sea, but populations in such areas are regarded as relict (Veith, 1997). It is a strictly nocturnal species, staying close to water but foraging on land, particularly after rain, for various invertebrates, and returning to its refuge by day. It is slow-moving, relying on the protection afforded by its noxious skin secretions. Its bright colouration probably acts as an efficient warning to would-be predators (Arnold and Burton, 1978).

Unusually, for European salamandrids, reproduction takes place on land. According to Arnold and Burton (1978), *S. salamandra* is generally oviparous, laying its eggs in damp places, but in Iberia and at high altitudes everywhere, it is viviparous and females give birth to fully-formed young. Veith (1997) claims that it is viviparous across its range, giving birth to fully developed larvae, and even metamorphosed juveniles in parts of Iberia and Corsica.

Its distribution spans west, central and southern Europe. It reaches about 54°N north in Germany and is absent from the lowlands bordering the North Sea (Gasc *et al*, 1997). It is also

Figure 2.1: *S. salamandra* and its distribution (after Gasc *et al*, 1997).

found in northwest Africa and some of southwest Asia, (Arnold and Burton, 1978; Gasc *et al*, 1997). *S. salamandra* is not present in the British Isles today, but an introduction was successful earlier this century at Heysham in Lancashire (Frazer, 1983), and unconfirmed reports have been made on East Anglian coastal dunes (C. Snell, pers. comm.). Though this species has never been reported as a British fossil, it must be considered as a potential Pleistocene colonist. Its preference for wooded upland areas, and its absence from lowland continental areas bordering the North Sea, seems to suggest a Pleistocene crossing via a low-lying land-bridge would be unlikely. However, the persistence of *S. salamandra* at Heysham shows that it can live in coastal areas. As appears to be the case for *R. dalmatina,* the current range of *S. salamandra* may have become restricted during the Holocene, due to forest clearance.

Genus: *Triturus* Rafinesque 1815

The genus *Triturus* is represented by the nine European species of newt, some of which extend into western Asia, and by three North American species. There are well over twenty recognised subspecies, and the systematics of the group, as stated by Smith (1969), is not yet fully agreed. They are typically relatively small, long-tailed, thin-legged, and fairly aquatic. They possess minute teeth, both on the jaws and on the palate, and catch food whilst on land by extending their sticky tongue. They are voracious feeders on a variety of invertebrates, as well as larvae of various amphibians. Breeding males develop a bright colouration and crests along the body and tail. Breeding normally requires still water, and occurs during the spring. Females lay single eggs, attaching them discretely to vegetation and other objects. The larvae are voracious carnivores (Arnold and Burton, 1978). The rate of larval development is controlled by ambient temperature, and is thus generally slower in Britain and other cooler parts of ranges. Though mortality is high before maturity, as in all amphibians, newts are still able to colonise suitable ponds and their surrounding habitat rapidly (Smith, 1969). Nevertheless, as they are relatively slow-moving in terrestrial habitats, the rate at which they cross land is likely to be less than that for anurans. As a group, the European newts have a wide-ranging distribution, with five Palaearctic species. Species density is greatest in a band running from central to northwestern France, where five species live sympatrically (Arntzen and De Wijer, 1989).

Triturus marmoratus (Latreille 1800) **Marbled newt**

The marbled newt is large, reaching up to 140mm, and occasionally larger (Arnold and Burton, 1978). It has a bright green and black marbled pattern, with a pale underside which is also mottled black. *T. marmoratus* has a very similar ecology to *T. cristatus*, but is less aquatic, and its range is much less extensive. According to Ovenden *et al* (1979), this species replaces *T. cristatus* in southwest Europe. *T. marmoratus* lives in a variety of habitats, often in fairly dry woods and heaths, tending to tolerate drier conditions than *T. cristatus* (Arnold and Burton, 1978). In parts of France, Arntzen and De Wijer (1989) found that *T. marmoratus* tended to occupy more hilly and

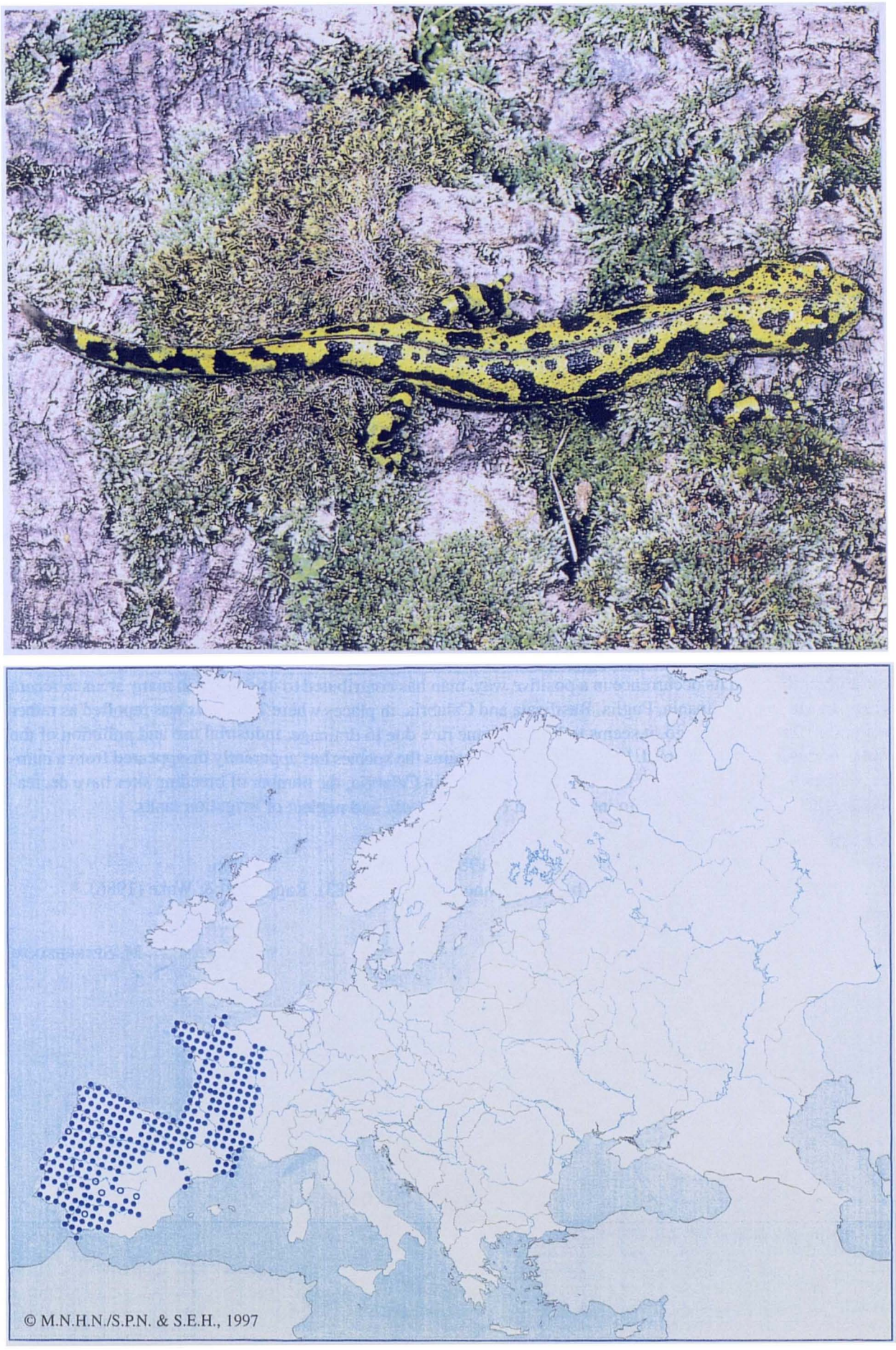


Figure 2.2: *T. marmoratus* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

forested areas than *T. cristatus*, and noted that these two species seem to be 'parapatric', living in different habitats whilst being regionally sympatric. Zuiderwijk (1997a) described the distribution of *T. marmoratus* and *T. cristatus* in Central France as 'mosaic-like'. Here, hybridization occurs readily where both species inhabit the same ponds, but this may have the effect of 'reproductive self-destruction', therefore perpetuating geographical isolation (Zuiderwijk, 1997a).

T. marmoratus has a southwest European range, covering Iberia and western France (Arnold and Burton, 1978; Gasc *et al*, 1997). It is not found in the British Isles, but extends along the northwest coast of France, in Brittany and Normandy, though with a restricted distribution in this area (Arntzen and De Wijer, 1989). There are currently no British fossil records of this species. Nevertheless, it is considered here as a potential Pleistocene colonist. Its preference for hilly areas may have prevented its crossing low land-bridges, but under different habitat distributions to those found today in northwest Europe, it may have had a different altitudinal distribution.

Triturus cristatus (Laurenti 1768) **Crested newt**

This is the largest European newt, females are slightly larger than males, often reaching 140mm in total length, and possibly up to 180mm (Arnold and Burton, 1978). Its colour is dark greyish brown above, with a yellow, orange or red underside with black spots. Breeding males develop a high frilled body and tail crest. There are four well-defined subspecies: *T. c. cristatus* (northern Europe including Britain), *T. c. carnifex, T. c. karelinii* and *T. c. dobrogicus*. This is a very variable species, and body and leg proportions, skin texture and colouration differ widely across its geographic range (Arnold and Burton, 1978). It is fairly aquatic, and can be found in water at any time of the year, though it is more terrestrial outside the breeding season (Arnold and Burton, 1978). On land, it tends to be found in damp places, hidden beneath objects, and often in wooded areas close to ponds. It can be found up to altitudes of 2,000m, becoming more montane in the south of its range (Arnold and Burton, 1978; Arntzen and Borkin, 1997). Its skin secretions may deter some predators, but annual mortality has been measured at 58% in adult populations (Frazer, 1983). *T. cristatus* usually hibernate on land, emerging in the spring when ground temperatures reach 5-7°C (Frazer, 1983). For successful reproduction, *T. cristatus* requires a body of shallow still or slow-moving water, typically containing an abundance of aquatic vegetation. It differs greatly in local abundance, according to suitability of habitats (Frazer, 1983).

T. cristatus is distributed across most of Europe, including Britain but not Ireland, and reaching to northern Sweden, south of the Arctic Circle (Gislén and Kauri, 1959; Arnold and Burton, 1978; Gasc *et al*, 1997). It also extends into parts of southern Finland where it reaches around 62°N (Gasc *et al*, 1997), and eastwards into Belorussia and Russia. It is absent from Iberia and southwest France, but reaches eastwards to east and central Asia and the Caucasus (Arnold and Burton, 1978). Where its range overlaps with *T. marmoratus*, it inhabits flatter lowland areas (Arntzen and De Wijer, 1989). *T. cristatus* has been described as a British fossil at Cudmore Grove, Barnham, Purfleet, Selsey and Bosley (Holman *et al*, 1990; Holman and Stuart, 1991;

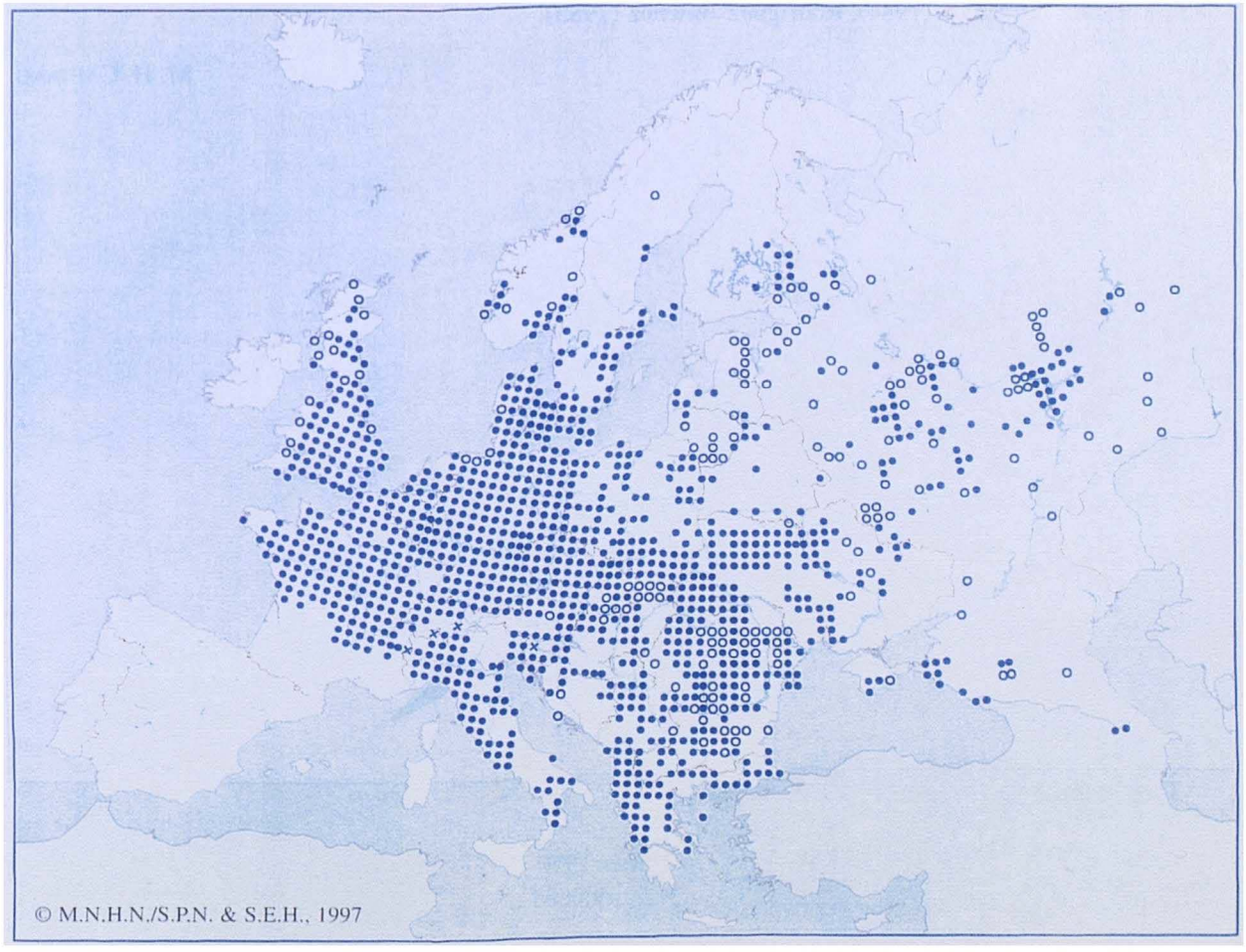


Figure 2.3: *T. cristatus* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

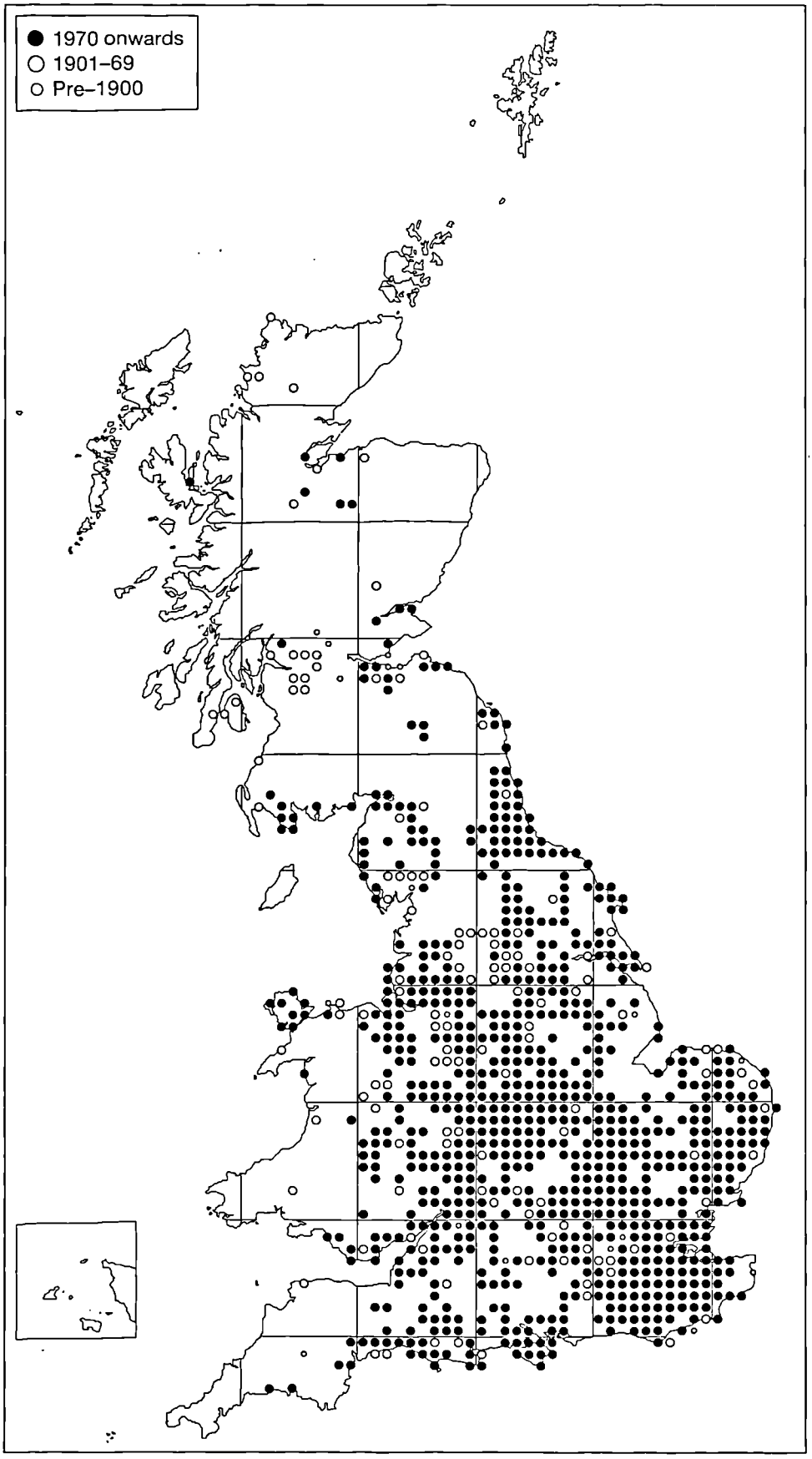


Figure 2.4: Distribution of *T. cristatus* in Britain (after Arnold, 1995).

Holman, 1992d; 1995b; Ashton *et al*, 1994). Its large distributional range might also mean that *T. cristatus* would have been better placed for surviving cold stages, and migrating into new areas during interglacials, than species with limited ranges, such as *T. marmoratus*. Its absence from Ireland may have been due to a lack of suitably mature vegetated ponds at the time of the last land-bridge. *T. vulgaris,* which is present in Ireland, is less particular about breeding sites.

Triturus alpestris (Laurenti 1768) **Alpine newt**

This newt is strikingly-coloured and may reach 120mm in length, with females being longest. The distinctive colouration is dark above, with a deep yellow to red belly, and spotted flanks, with a bluish band along each side. It is a very aquatic species, rarely found out of water. In the southern parts of its range it is strictly montane, reaching altitudes of c.2,500m in the Alps (Arnold and Burton, 1978; Zuiderwijk, 1997b). However, it is a highly flexible species, and may be found at altitudes as low as 3m (Zuiderwijk, 1997b). In the north of its range, it occupies a wide variety of habitats, particularly shaded lowland ponds in decidous woodland (Arnold and Burton, 1978; Ovenden *et al*, 1979; Bringsøe and Mikkelsen, 1993). In southern Denmark, it is only found in association with open deciduous forests, apparently unable to colonise cultivated land further north (Bringsøe and Mikkelsen, 1993). During its terrestrial phase, it inhabits cool, moist places such as dense herbage and leaf litter (Ovenden *et al*, 1979).

Its range mainly covers central Europe, parts of northern Italy, the Balkans, the Carpathians, and western Russia, the northern limit crosses southern Poland and most of Germany, parts of Denmark, and the low countries. It is absent from Iberia and much of southern and western France, but occupies eastern France, extending also along the northern coast, including Normandy and Brittany (Arnold and Burton, 1978; Gasc *et al*, 1997). A number of introduced colonies have persisted successfully in Britain. In Surrey, a colony survived for several decades, as did an introduction in Shropshire (Frazer, 1983). A population in Brighton has also bred for over twenty years in a garden pond (Beebee, 1995). As far north as Sunderland, introduced populations bred successfully and may have spread locally (Banks, 1989). These populations are apparently not affected by competition from other newt species and there are probably no ecological barriers to its spread (Frazer, 1983). The continental northern limit of the species is in southeast Jutland, Denmark, though this is not restricted by climate but by land use (Bringsøe and Mikkelsen, 1993). It seems that the British climate, even the cool summers of northeast England, is suited to *T. alpestris*, and geographic isolation is probably the only barrier to colonisation of Britain. Its absence might suggest that its dispersal was limited by a lack of deciduous woodland, whilst a land bridge still existed.

During the Pleistocene, *T. alpestris* would have been most likely to reach Britain during a prolonged period of connection to the continent, provided that a corridor of suitable habitat was available. Recent re-examination of the Boxgrove material (see Chapter 6) has identified the first British fossil record of *T. alpestris*.

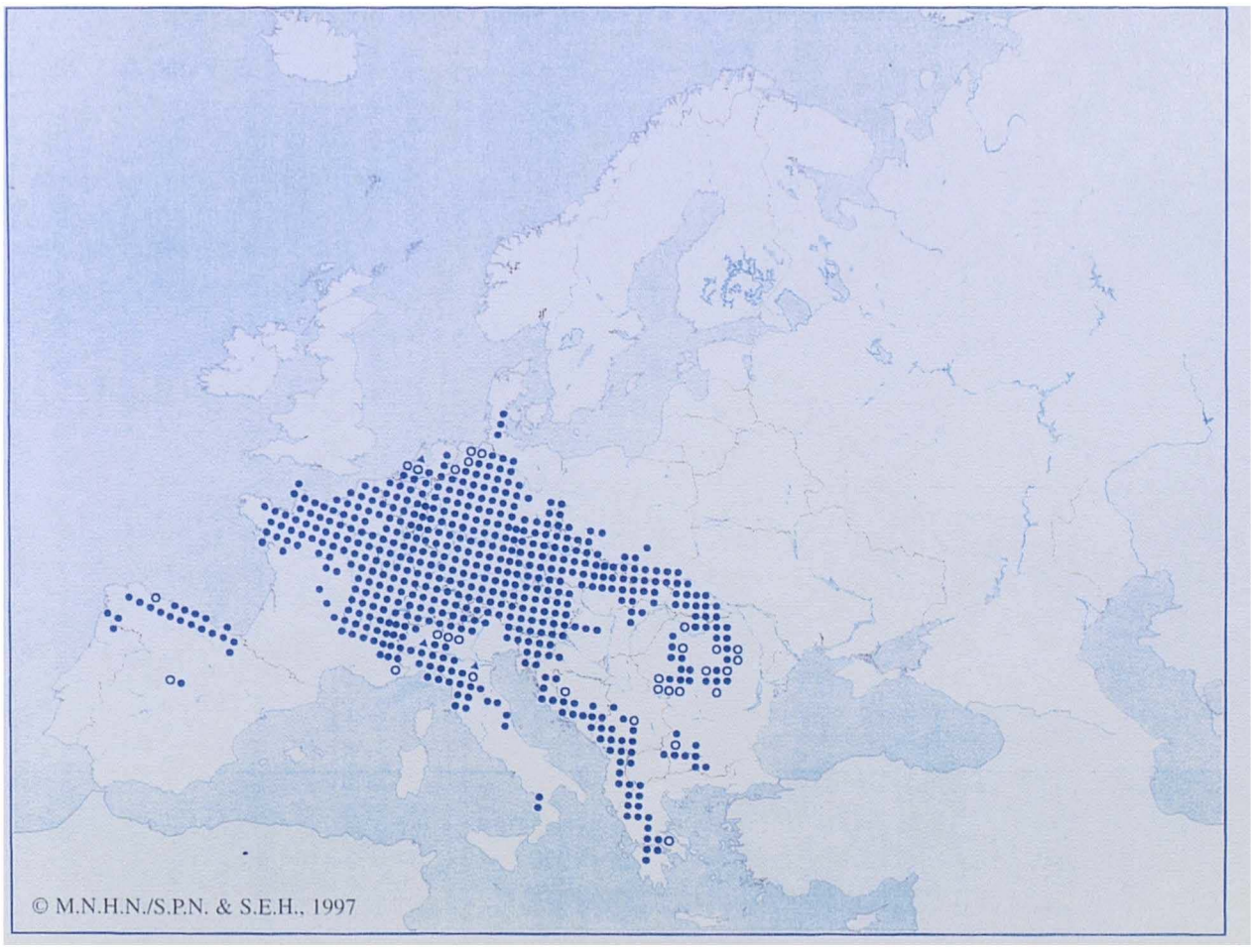


Figure 2.5: *T. alpestris* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

Triturus vulgaris (Linnaeus 1758) **Smooth newt**

This is a widely-distributed and very variable species, and the commonest newt in most of its range (Arnold and Burton, 1978; Kuzmin and Zuiderwijk, 1997). In length, the slightly larger males can reach 110mm, but populations in the south Balkans rarely reach 75 mm (Arnold and Burton, 1978). Thus, it seems to be at its optimum in the north. There are four recognised subspecies which probably originated from Pleistocene episodes of isolation (Kuzmin and Zuiderwijk, 1997). It has a drab olive-brown colour above, with an orange belly, spotted or striped with black markings. *T. vulgaris* is probably the most terrestrial European species, occupying a wide variety of habitats, including open farmland, urban areas, hedgerows and leaf litter in woods (Arnold and Burton, 1978). Food consists of a range of terrestrial and aquatic invertebrates, including slugs and snails, but also frogspawn and tadpoles of frogs and newts, but not those of toads (Frazer, 1983). For reproduction, smooth newts prefers weedy ponds and ditches which are moderately unshaded, but may breed in a range of shallow water bodies, including muddy plant-free ponds (Arnold and Burton, 1978). There is evidence that it actually prefers water with relatively high concentrations of certain heavy metals such as potassium (Frazer, 1983).

Females become more productive with age and some populations are known to breed twice a year (Frazer, 1983). Its reproductive cycle is fairly rapid, but larvae are eaten by sticklebacks and caddis fly larvae, and mortality is high throughout the developmental stages. Metamorphosing larvae are also vulnerable to capture by water shrews (Frazer, 1983). This is a long-lived species and breeding females have been recorded to reach thirteen years old (Frazer, 1983). *T. vulgaris* is essentially a lowland species, but may be found up to 1,000m, and possibly up to 2,000m in the south of its range (Arnold and Burton, 1978).

Its distribution is similar to that of *T. cristatus*, and spans from western France, across Europe, into western Asia. It ranges north ito 64°N in Scandinavia, reaching the head of the Gulf of Bothnia (Arnold and Burton, 1978; Gasc *et al*, 1997), but not entering the Arctic Circle (Smith, 1969). Sufficiently warm summer temperatures are most important for its survival. Although it is distributed widely in Britain, it is less common than *T. helveticus* in Wales and Scotland (Smith, 1969). Assuming that it arrived naturally (there is no evidence to the contrary), *T. vulgaris* is the only newt to have reached Ireland before its isolation from Britain, perhaps due its ability to breed in a wider range of ponds. From its modern distribution, *T. vulgaris* appears to be more cold -tolerant than *T. helveticus*, but not necessarily more so than *T. cristatus*. In Pleistocene situations, the absence of one or more newt species might provide more useful information than the presence of the other newts. Remains of *T. vulgaris* are known from West Runton, Cudmore Grove, Barnham, Shropham and Whitemoor Channel (Holman *et al*, 1988; 1990; Holman and Clayden, 1990; Holman and Stuart, 1991; Ashton *et al*, 1994). After recent re-examination, the record from Boxgrove (Holman, 1992a) is considered to be incorrect (see Chapter 6).

Figure 2.6: *T. vulgaris* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

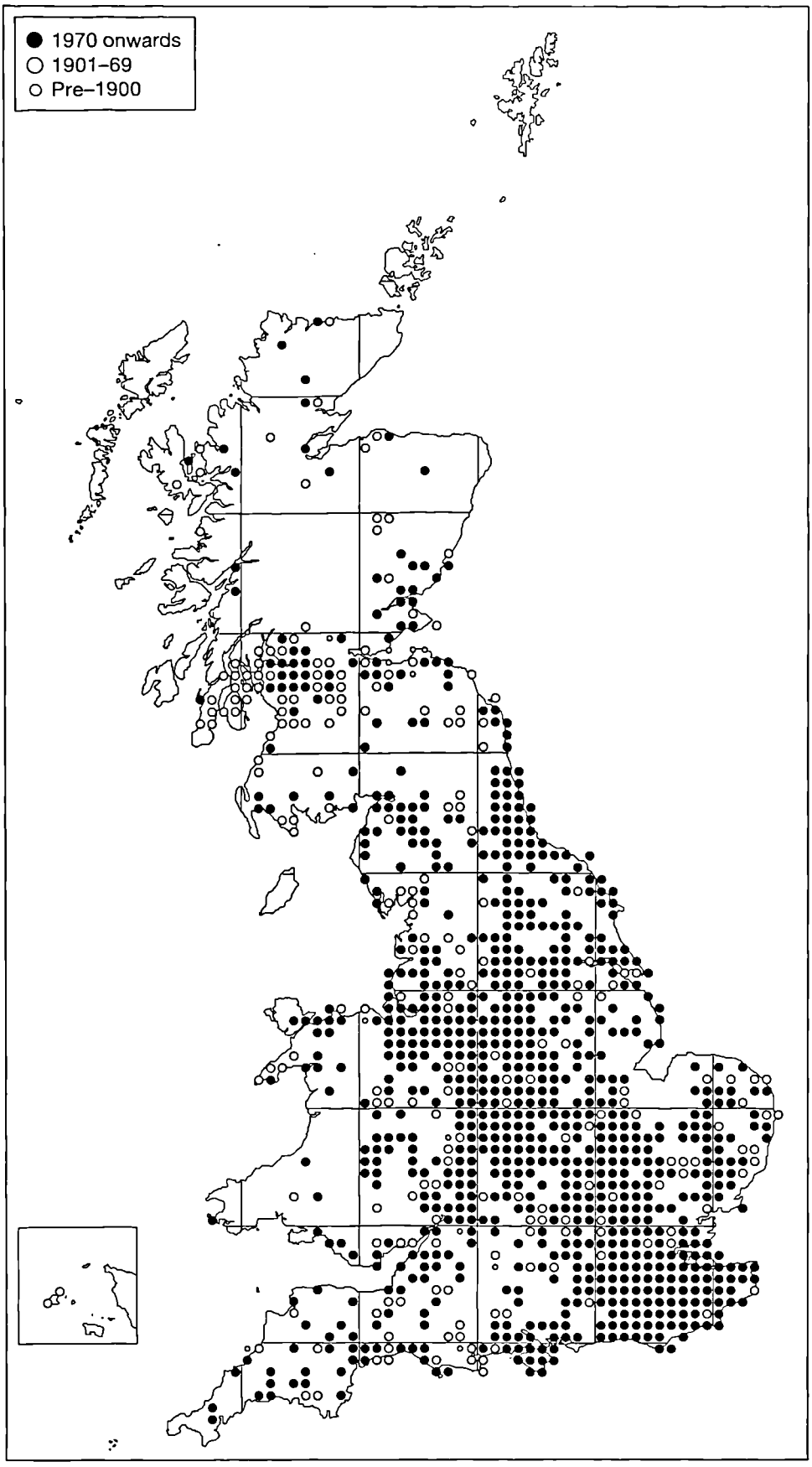


Figure 2.7: Distribution of *T. vulgaris* in Britain (after Arnold, 1995).

Triturus helveticus (Razoumowski 1788) **Palmate newt**

T. helveticus is a small newt: generally less than 90mm in total length, with a shorter and rounder than *T. vulgaris*, though its olive drab colour gives the two species a very similar appearance. Breeding males have a low straight-edged crest along the back and tail, ending in a thin filament measuring 4-7 mm, and strongly webbed hind feet (Smith, 1969). It is a more aquatic species than *T. vulgaris*, and may be found in water at any time of the year, possibly overwintering in ponds (Smith, 1969; Frazer, 1983). It inhabits a wide range of water-bodies including woodland ponds and puddles, heathland pools and bogs, running water, and in coastal areas, brackish pools (Arnold and Burton, 1978). It is widespread in wetter western areas of Britain (Smith, 1969) and may breed in the shallow margins of oligotrophic mountain lakes, preferring clearer and more acid water than *T. vulgaris* (Arnold and Burton, 1978). It can tolerate low nutrient levels and is less common in calcareous areas, though populations are known from chalk ponds (Frazer, 1983).

T. helveticus has a subatlantic distribution (Zuiderwijk, 1997c). It is restricted to northwest Europe, spanning from northern Iberia through France and western Germany, but absent from most of the Netherlands. It is present throughout Britain, but not Ireland, Denmark or Scandinavia (Arnold and Burton, 1978; Gasc *et al*, 1997). Populations are also known on the islands of Bardsey, Skokholm and Skomer, off the Welsh coast, and on 'many of the islands off the west coast of Scotland' (Smith, 1969). It is mainly an upland species in the south of its range, reaching 1,000m in the Alps, and 2000m in the Pyrenées (Arnold and Burton, 1978). In Britain it is commonest in upland areas, particularly in Wales and the west of Scotland. It may be found from sea-level to 880m, but in lowland areas it is more particular about its choice of ponds (Frazer, 1983). It is the commonest species of newt in France, in the centre of its range (Smith, 1969).

Glacial refugia are believed to have centred on southern France and/or Northern Spain (Zuiderwijk, 1997c). Since the last glaciation, *T. helveticus* was able to reach islands off the west coast of Britain, before land connections were drowned, but does not appear to have reached Ireland. This absence suggests that it reached Britain later than *T. vulgaris* or that environments were not suited to it. It crossed to islands off the coast of Scotland before they were isolated in the early to middle Holocene.

Remains of *T. helveticus* have been identified at Barnham and Whitemoor Channel (Ashton *et al*, 1990; Holman and Stuart, 1991), and possibly also at Tiddington (Holman, 1992c).

Order: Anura Rafinesque 1815

The order Anura, the frogs and toads, are tailless amphibians with elongate hindlimbs. The feet have proximal tarsal elements elongated and fused at their ends, superficially similar to the hind feet of quadruped mammals. The trunk is rigid and short, normally with only eight presacral vertebrae and no ribs, except in some primitive families (e.g. Discoglossidae). The head is immovable and relatively very large. Females lay their eggs in large bundles or strings, and the

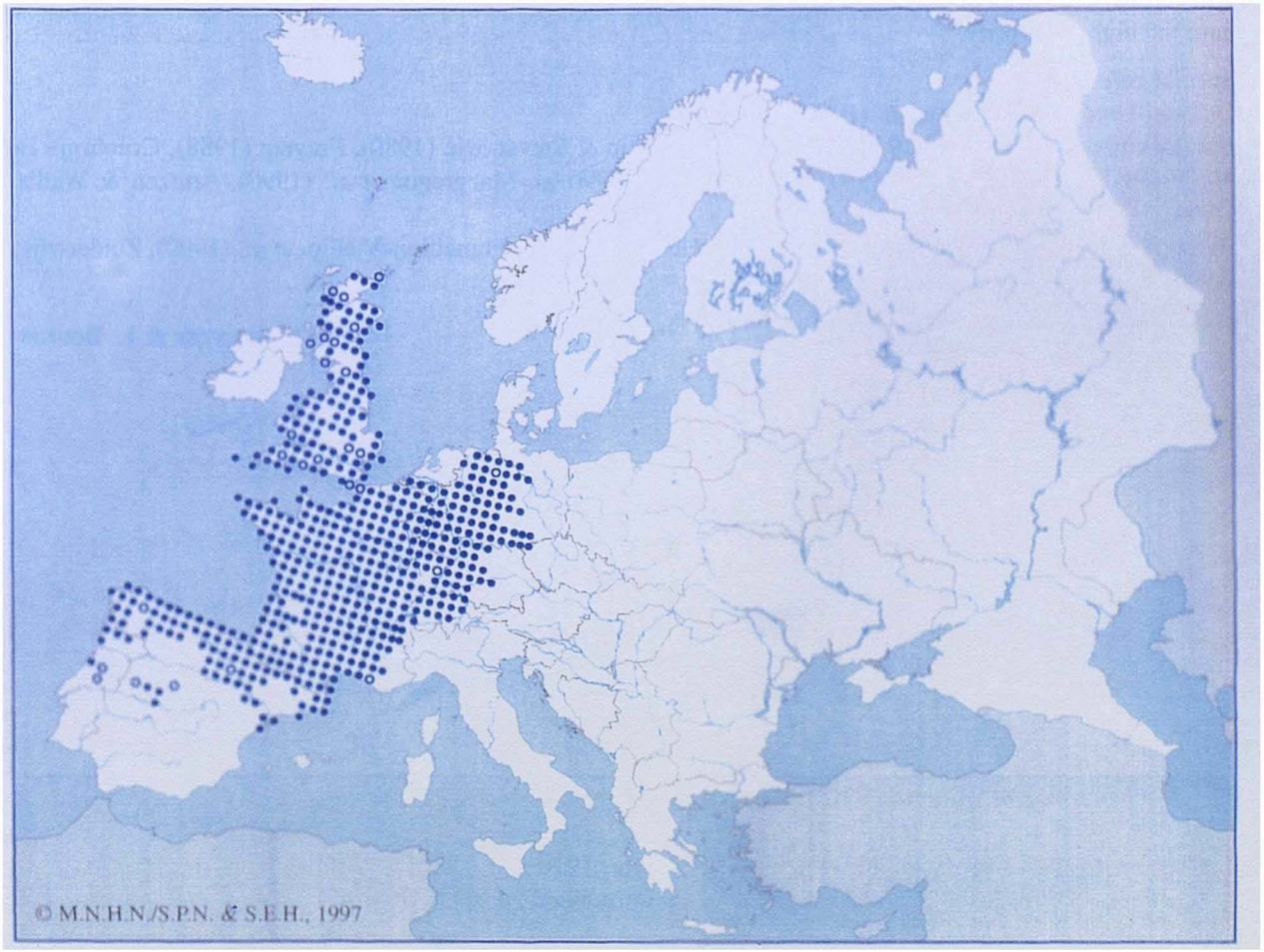


Figure 2.8: *T. helveticus* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

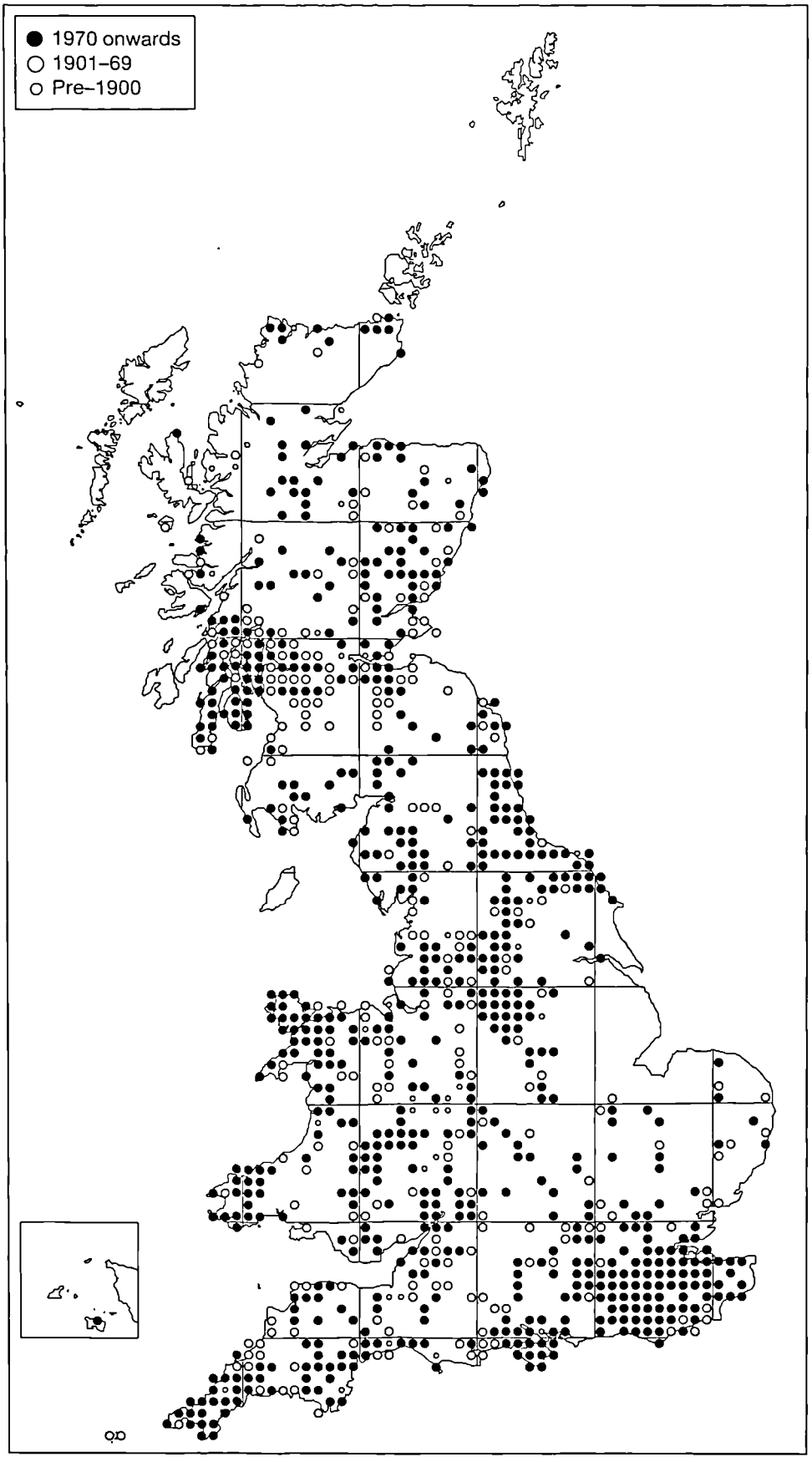


Figure 2.9: Distribution of *T. helveticus* in Britain (after Arnold, 1995).

young develop as aquatic tadpoles until metamorphosis. Seventeen species are considered here.

Family: Discoglossidae Günther 1859

This is a rather primitive family of toads, predominantly European, with seven of the ten species in that area. Their name derives from the disc-shaped tongue, which cannot be protruded to catch food (unlike most other anurans). Females can lay two or three broods of eggs a year (Arnold and Burton, 1978).

Bombina variegata (Linnaeus 1768) Yellow-bellied toad

This is a small (less than 50mm), warty and very aquatic toad, with a distinctively flattened body and head, with no eardrums. It is brown or olive above, with spiny warts, and its underside is bright yellow, with an irregular marbled black pattern. It is distasteful to most predators, and deters them by displaying its yellow underside. It is usually active during the day, and less aquatic than *B. bombina* (Necas *et al*, 1997). It inhabits a variety of shallow water bodies including stream and river edges, marsh pools, ditches, ponds and temporary puddles (Arnold and Burton, 1978), but typical habitats are unshaded, temporary pools in or near forests (Gollman *et al*, 1997b). It is gregarious, and will often gather in large numbers in ponds during the breeding season. Females normally lay less than 100 eggs, and the young develop rapidly. In Central Europe, it is strongly associated with wooded areas, with an altitude of c.250m to over 1,200m (Necas *et al*, 1997). Where its range overlaps with *B. bombina*, *B. variegata* is confined to more upland areas (Arnold and Burton, 1978).

Its range covers much of central and southern Europe, though not Iberia and the south Balkans. Its northern limit extends across northern France, central Germany, southern Poland and to the Black Sea coast (Arnold and Burton, 1978; Gasc *et al*, 1997). Isolated populations around the Gironde in France form its western limit. During glacial episodes, its refugia were probably in southern European mountains, particularly in the Balkan peninsula (Gollman *et al*, 1997b).

There are currently no British fossil records of this species. *B. variegata* is present along much of the adjacent French coast, and might be considered a potential Pleistocene immigrant to the British Isles.

Bombina bombina (Linnaeus 1761) Fire-bellied toad

B. bombina is a small, warty and aquatic toad, similar to *B. variegata*. Its flattened body is usually blackish above, and its belly is marbled with a network of bright red or orange markings. According to Arnold and Burton (1978), it lives in similar habitats to *B. variegata*, but Gollman *et al* (1997a) associate it more with swamps and floodplains than wooded areas. In some regions, forest clearance and pond creation, during historic times, may have allowed *B. bombina* to expand its range (Gollman *et al*, 1997a). It is often found in permanent ponds and larger lakes than *B. variegata*, where it breeds in dense offshore vegetation (Necas *et al*, 1997). Arnold and Burton

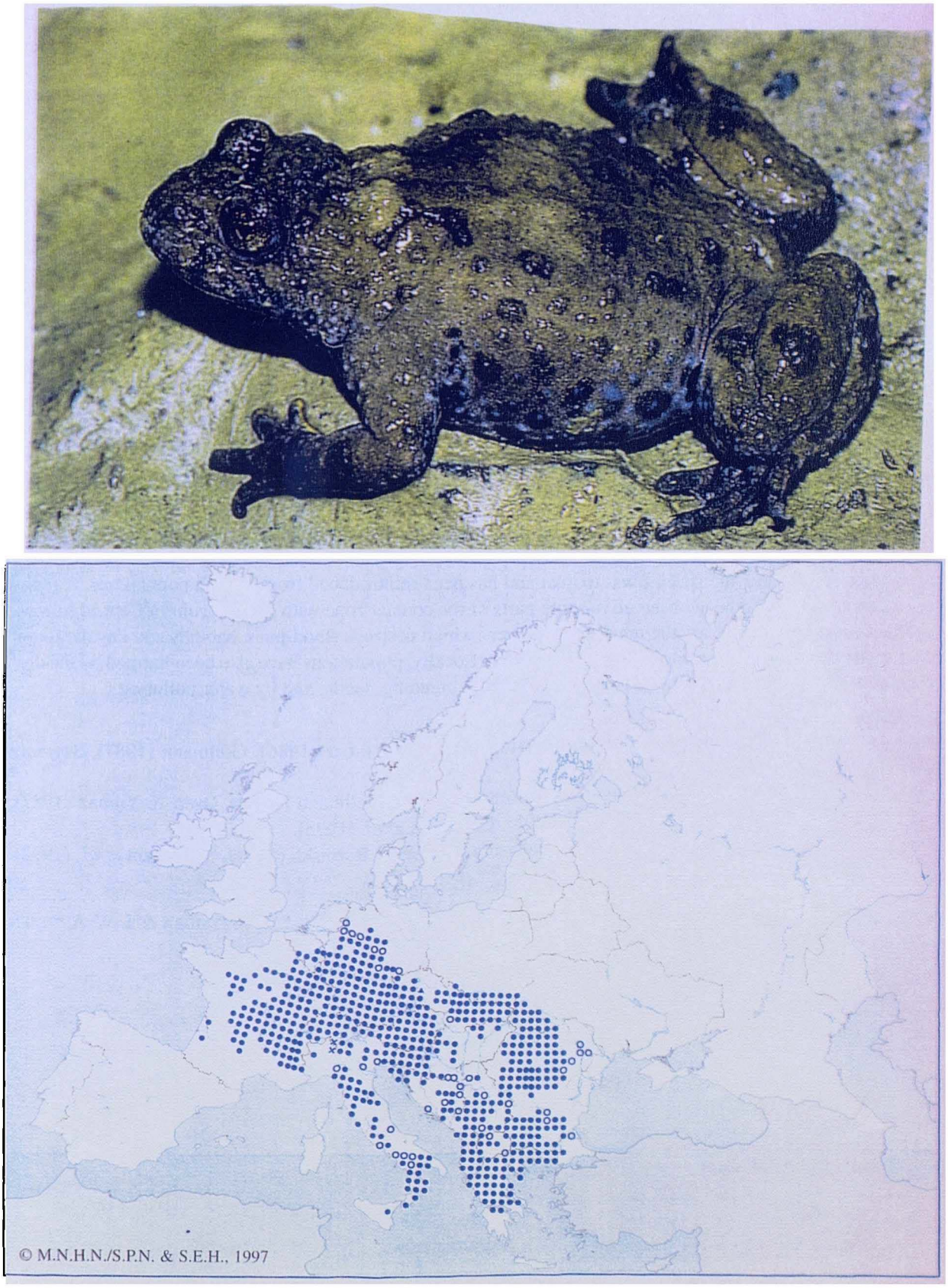


Figure 2.10: *B. variegata* (after Necas *et al*, 1997) and its distribution (after Gasc *et al*, 1997).

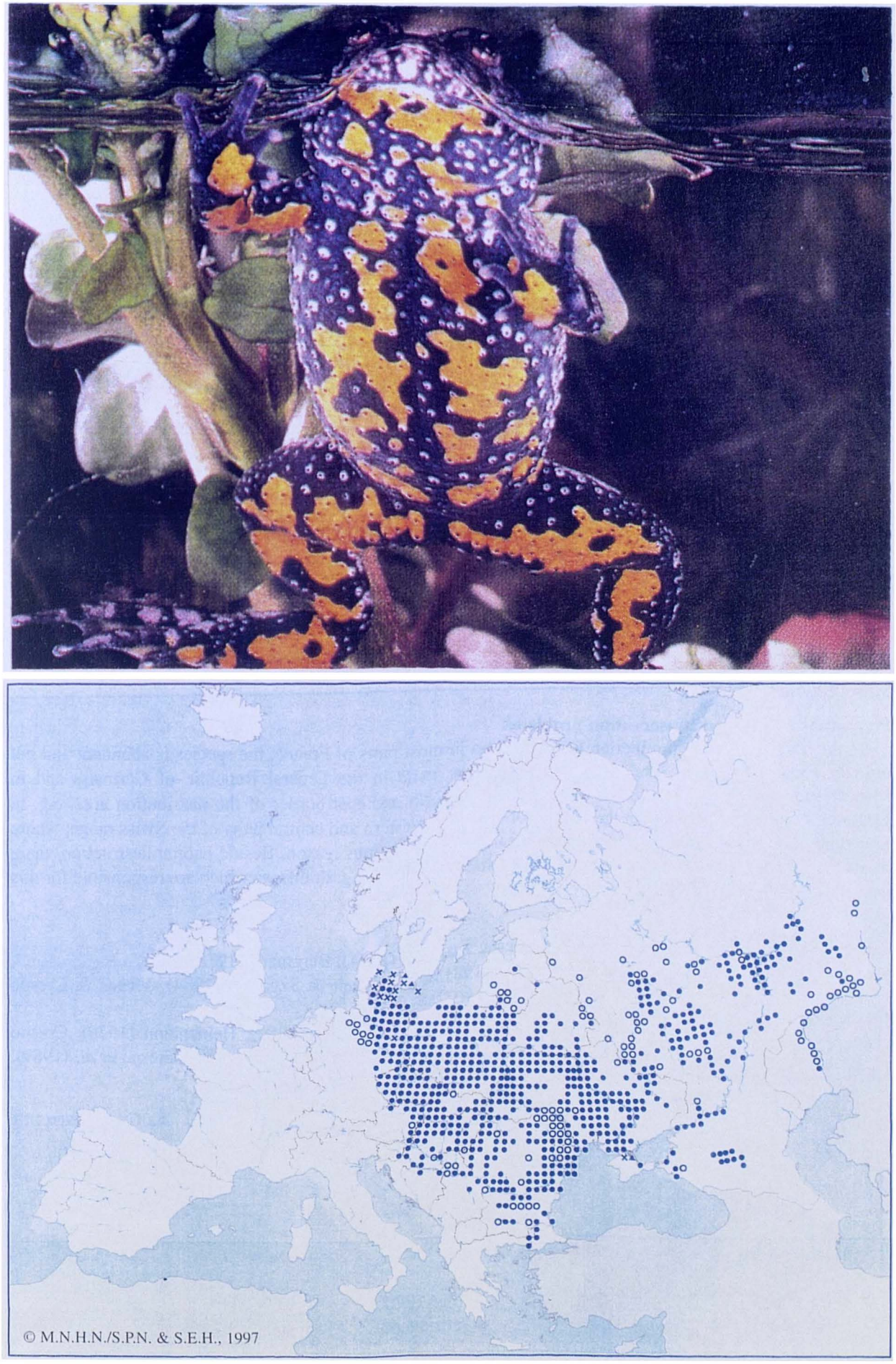


Figure 2.11: *B. bombina* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

(1978) reported that it is an exclusively lowland species, but Necas *et al* (1997) suggested that it is found up to 730m elevation. It is more aquatic than *B. variegata*, and found in both meadows and forested area alike (Necas *et al*, 1997). A band of sympatry with *B. variegata* runs across eastern Europe, but otherwise their ranges are mutually exclusive.

B. bombina has an eastern distribution, extending from eastern Europe to western Asia, but absent from southern Europe (Arnold and Burton, 1978; Gasc *et al*, 1997). Its range spans across the Baltic states and Belorussia, extending around the Baltic coast to Denmark. It became extinct in southern Sweden, but has been reintroduced in Scania (Arnold and Burton, 1978; Gollman *et al*, 1997a; Gislén and Kauri, 1959). Its northern limits are around 56°N (Gasc *et al*, 1997), and are probably determined by summer temperatures (Gollman *et al*, 1997a). Glacial refugia may have been in steppe regions around the Black and Caspian Seas (Gollman *et al*, 1997a).

There are currently no British fossil records of this species. *B. bombina* is not found in Britain, but reaches some of the southern North Sea coast in Germany and Denmark.

Alytes obstetricans (Laurenti 1768) **Midwife toad**

Less than 50 mm in length, this is a small, plump toad: usually grey, olive or brown above, with darker spots, and a pale underside. It lives in a range of habitats from woodlands to gardens and cultivated areas, often in rocky areas and screes, up to 2,000m elevation (Arnold and Burton, 1978). All types of ponds and pools are frequented, and even rivers and streams, particularly in Iberia (Grossenbacher, 1997a). *A. obstetricans* can burrow, and will hide by day in holes and crevices (Arnold and Burton, 1978), with a warmer microclimate than outside (Grossenbacher, 1997a). Unlike most other European anurans, mating takes place on land, and the male carries the sixty or so fertilised eggs around his back legs. They are kept moist by occasional immersion in water and, when ready to hatch, they are deposited in shallow water. Like those of *Bombina*, the young develop rapidly.

Its distribution is west European, mainly covering Iberia and France, with a band extending across the Alps and much of Germany, and a northern limit from Germany to the Straits of Dover (Arnold and Burton, 1978; Gasc *et al*, 1997). It is very common throughout much of its range, but is absent from lowland plains in the north (Grossenbacher, 1997a). It is not native to Britain, but has been successfully introduced. It is present throughout France, including all of the adjacent Channel coast and could be expected as a Pleistocene colonist. There are currently no British fossil records of this species.

Family: Pelobatidae Bonaparte 1850

Subfamily: Pelobatinae Bonaparte 1850

This is also a somewhat primitive family, superficially resembling the typical toads *Bufo*. Their distribution covers Europe, northwest Africa and western Asia (Arnold and Burton, 1978). The tadpoles of pelobatids are very large, and may grow to 100mm, and even up to 175mm (Arnold

Figure 2.12: *A. obstetricans* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

and Burton, 1978). There are three European species, of which two are considered here.

Pelobates cultripes (Cuvier 1829) **Western spadefoot**

Pelobates cultripes can reach 100mm in length, with a plump and smooth-skinned body. Its colour is yellowish or whitish, with olive green blotches or speckles. The head is broader and noticeably less domed than *Pelobates fuscus*. It is often associated with sand-dunes and may be found in large numbers on sandy coasts (Arnold and Burton, 1978; Lizana, 1997). It also inhabits open marshland with shallow water, and other areas with light soils (Arnold and Burton, 1978; Morrison, 1994). It digs long vertical burrows with the large, sharp-edged 'spades' on its hind feet (Arnold and Burton, 1978). Its distribution is restricted to areas with mild winters and enough rainfall to supply permanent ponds, and its fossorial habits restrict it to soft sandy soils (Lizana, 1997). It is strictly nocturnal, emerging usually after heavy rainfall. During the breeding season, eggs are wrapped around submerged aquatic vegetation (Morrison, 1994).

It ranges across Iberia, and parts of southern France, with disjunct populations in western France, around the Gironde Estuary and parts of the Loire Valley (Gasc *et al*, 1997). *P. cultripes* can be recognised as a distinct species as far back as the Pliocene (Lizana, 1997). Its Postglacial expansion apparently reached France via Cataluña (Lizana, 1997), thus it probably followed the Garonne Valley. Habitat destruction (Lizana, 1997) probably explains the northern relict populations. There are currently no British fossil records of this species.

Pelobates fuscus (Laurenti 1768) **Common spadefoot**

P. fuscus reaches around 80mm in length, with males being smaller than females, and is plump and smooth-skinned. Colour is very variable from light to dark, taking in a range of greys, browns, yellow and whitish shades, but usually with darker speckling or marbling. It may also have a covering of small orange spots above, particularly around its sides. Its head is narrower and more domed than *P. cultripes*. *P. fuscus* is said to smell strongly of garlic and is also known as the garlic toad (Arnold and Burton, 1978; Morrison, 1994). It is mainly nocturnal, moves by hopping, and usually ventures out after wet weather. It hides in deep, almost vertical burrows excavated with its hind feet (Ovenden *et al*, 1979). It has an impressive defense posture where it stands high on its four legs, inflates itself and often jumps forward at its attacker, with its mouth agape (Arnold and Burton, 1978). *P. fuscus* is a lowland species, reaching from sea-level to 800m (Nöllert, 1997). It breeds during the spring in deep pools and ditches, where the eggs are laid around the stems of aquatic plants (Arnold and Burton, 1978; Necas *et al*, 1997).

Its range extends across central and eastern Europe to the Urals. It is absent from southern and western Europe (Gasc *et al*, 1997). Its northern limit extends into Denmark (to 57°N), the southern tip of Sweden and the Russian coast of the Gulf of Finland (60°N) (Nöllert, 1997). Arnold and Burton (1978) showed its range covering most of France, but it is in fact absent from all of France except Alsace (Gasc *et al*,1997).

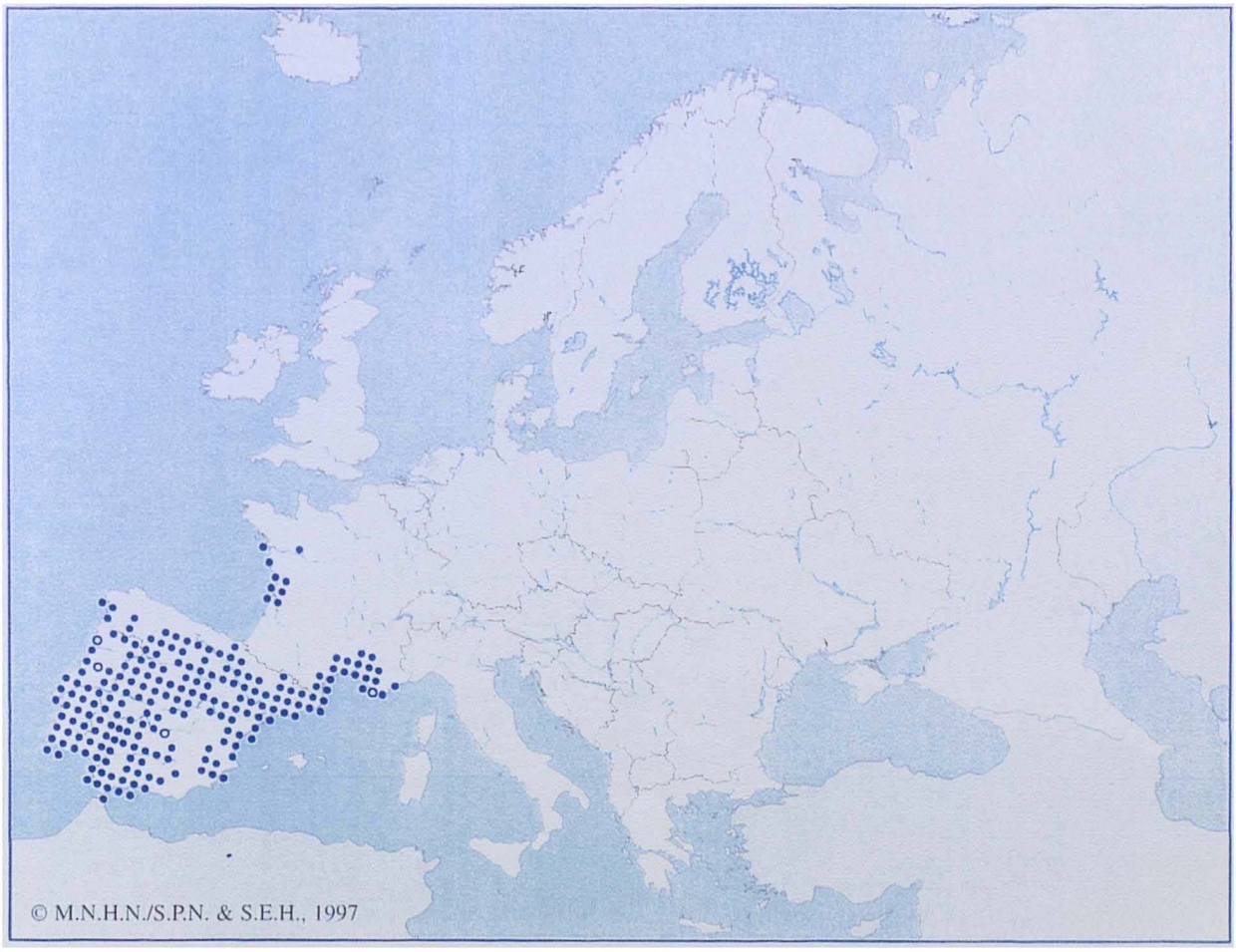


Figure 2.13: *P. cultripes* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

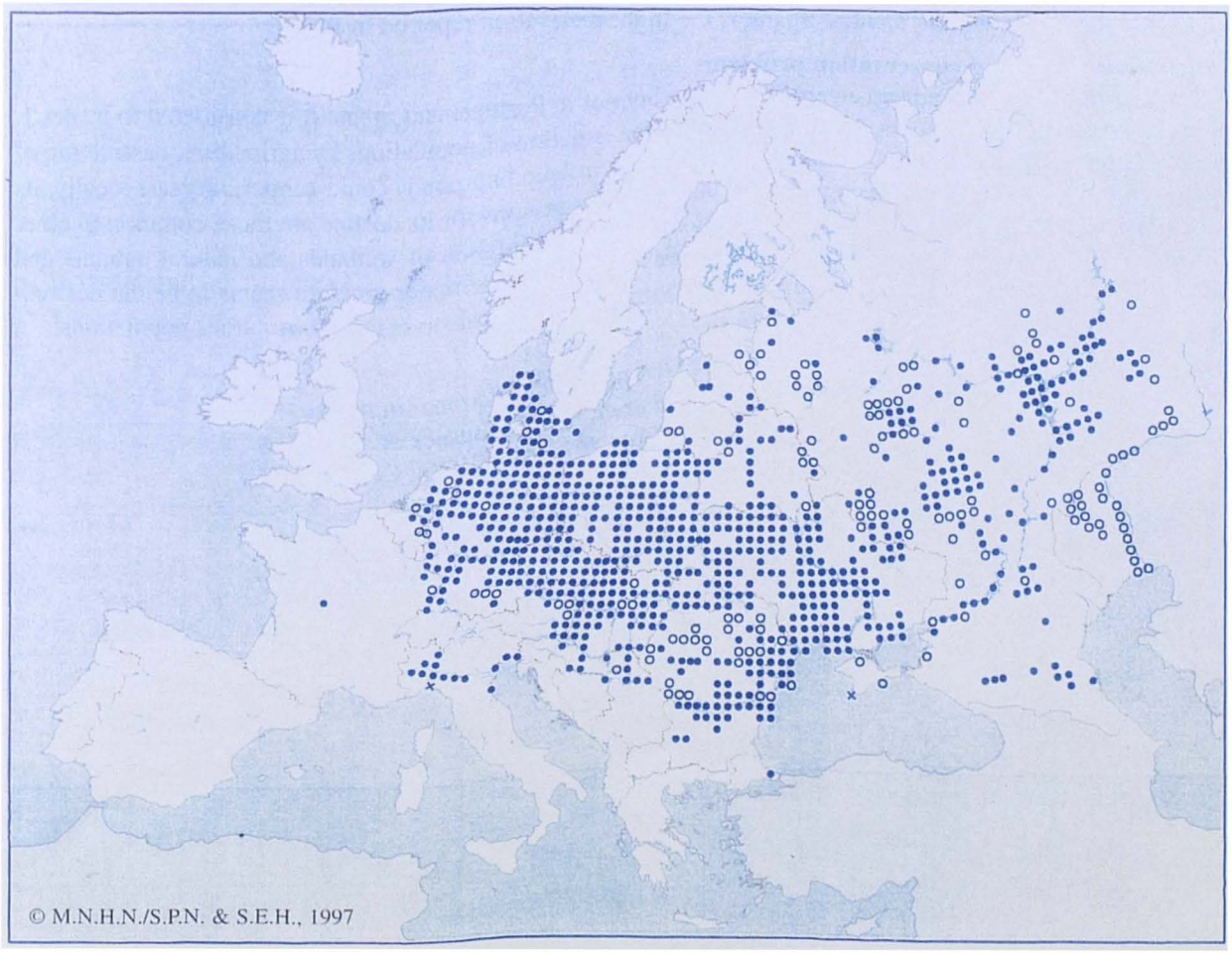


Figure 2.14: *P. fuscus* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

It is absent from the British Isles, but reaches the Channel coast and much of the North Sea coast of continental Europe. Spawn which apparently belonged to *Pelobates* has been identified from a pond in South Wales (Griffiths, 1987). It is not known if there was a local introduction, but other introductions in England have failed (Nöllert, 1997). Holman (1992a) recorded *P. fuscus* from Boxgrove. After recent re-examination, this record is considered to be correctly identified (see Chapter 6).

Family: Pelodytidae Bonaparte 1850

The Pelodytidae are small toad-like anurans, with fossorial habits. Some workers consider them to be a subfamily of the Pelobatidae, but they differ in a number of skeletal characteristics (Duellman and Trueb, 1986).

Pelodytes punctatus (Daudin, 1802) **Parsley frog**

A small, but agile and long-limbed animal, reaching around 50mm in length. It is pale grey to olive above, with bright green spots, and smells strongly of garlic (Arnold and Burton, 1978). It is nocturnal largely terrestrial outside the breeding season, and can climb smooth, steep surfaces by using its abdominal surface as a sucker (Boulenger, 1897-8; Arnold and Burton, 1978). Little is known of its biology, but it is found in water bodies ranging from deep ponds to shallow pools. It prefers stony areas with small streams and sandy soils, and is associated with coastal dune slacks in northern France (Guyétant, 1997). According to Arnold and Burton (1978), it breeds in deep still-water pools which are generally well-vegetated; more particularly, Guyétant (1997) noted an association with oligotrophic conditions. Females often lay more than one brood of eggs per year, in aquatic vegetation (Arnold and Burton, 1978; Guyétant, 1997).

Its distribution is western European, covering Iberia and almost all of France, with slight extensions into neighbouring areas (Arnold and Burton, 1978; Gasc *et al*, 1997). It is not now found in the British Isles but *P. punctatus* was recorded from Westbury-sub-Mendip (Holman, 1993a), where it appears to have been a very early arrival to the interglacial fauna, but was absent in upper layers (see Chapter 8). *P. punctatus* could justifiably be compared to *B. calamita* in aspects of its ecology and pioneering status. These species have very similar ranges, and, like *B. calamita*, *P. punctatus* commonly inhabits coastal dune systems (Guyétant, 1997).

Family: Bufonidae Gray 1825

The family Bufonidae, or typical toads, are widely distributed in temperate and tropical regions (Frazer, 1983). They have thick, glandular skin, often with pustular warts (Duellman and Trueb, 1986). Some genera, including *Bufo* have large parotoid glands on the head. Toads are largely nocturnal, except during the breeding season when they often gather diurnally, in large numbers in ponds (Arnold and Burton, 1978).

Figure 2.15: *P. punctatus* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

Bufo bufo (Linnaeus 1758) **Common toad**

This is the biggest European toad, with females reaching up to 150mm in length in the south of its range (Arnold and Burton, 1978). Its colour is generally brownish above, with a pale marbled underside. *B. bufo* is a very terrestrial species, and often lives in very dry places. It is ubiquitous throughout its range, occupying a very wide variety of habitats. It is often associated with coastal habitats, and was recorded in rockpools in Denmark, with a salinity of 8.36 parts per thousand (Johnsen, 1946). It is active nocturnally, and typically spends the day in a habitual refuge, often for many years (Arnold and Burton, 1978). It uses a characteristic defence posture, raising its body on fully-stretched legs, to increase its apparent size to predators. Mating takes place in still water or sometimes streams, often with thousands of toads gathering in one location (Arnold and Burton, 1978; Necas *et al*, 1997), where females lay several thousand eggs in strings. Tadpoles of *B. bufo* inhibit the growth of *B. calamita* tadpoles developing in the same pond, by excretion of an alga in their droppings. Where it is found sympatrically with *R. temporaria*, it is often associated with deeper, less well-vegetated ponds. *B. bufo* has been found to breed at salinities of up to 4.2 parts per thousand (Johnsen, 1946).

B. bufo has a Palaearctic distribution, present in virtually all of Europe but significantly absent from some large islands, including Sardinia and Corsica. It is also found in northwest Africa (*B. bufo spinosus*), and across Asia to Japan (Arnold and Burton, 1978; Bons and Geniez, 1996; Borkin and Veith, 1997; Gasc *et al*, 1997). In Central Europe it reaches 1,400m (Necas *et al*, 1997), but is mostly associated with lowland habitats. It reaches north into most of Scandinavia, and is found throughout Britain, but not Ireland.

There are fossil records of *B. bufo* from West Runton, Barnfield Pit (Swanscombe), Boxgrove, Cudmore Grove, Barnham, Hoxne, Nazeing, Purfleet, Selsey, Swanton Morley, Itteringham, Cow Cave, Ightham, Happaway Cave, Dog Holes, Creag nan Uamh, Whitemoor Channel, Barclodiad y Gawres, Tiddington and Repton (Newton, 1894; 1917; Allison *et al*, 1952; Pumphrey, 1956; Holman, 1985; 1987b; 1987c; 1988; 1989; 1992a; 1992b; 1992c; 1992d; 1993b; Holman and Clayden, 1988; Holman *et al*, 1988; 1990; Hallock *et al*, 1990; Raxworthy *et al*, 1990; Holman and Stuart, 1991; Ashton *et al*, 1994).

Bufo calamita Laurenti 1768 **Natterjack toad**

This robust, shortlimbed toad tends to be around 70-80mm in length, with females occasionally reaching 100mm (Arnold and Burton, 1978). It is brownish green or grey above, with darker markings overlaid, and a thin yellow vertebral stripe. The types of habitats it occupies vary significantly across its range, but it shows a marked preference for dry sandy or stony soils (Beebee, 1979). In the north of its range, it is more restricted to sandy heaths, coastal sand dunes and brackish marshes. In these parts of its range, it requires open, unshaded terrain to maximise summer insolation. Further south and east, where Mediterranean and continental summers are warmer, it occupies a wider variety of habitats (Beebee, 1979). Still, there is an association with

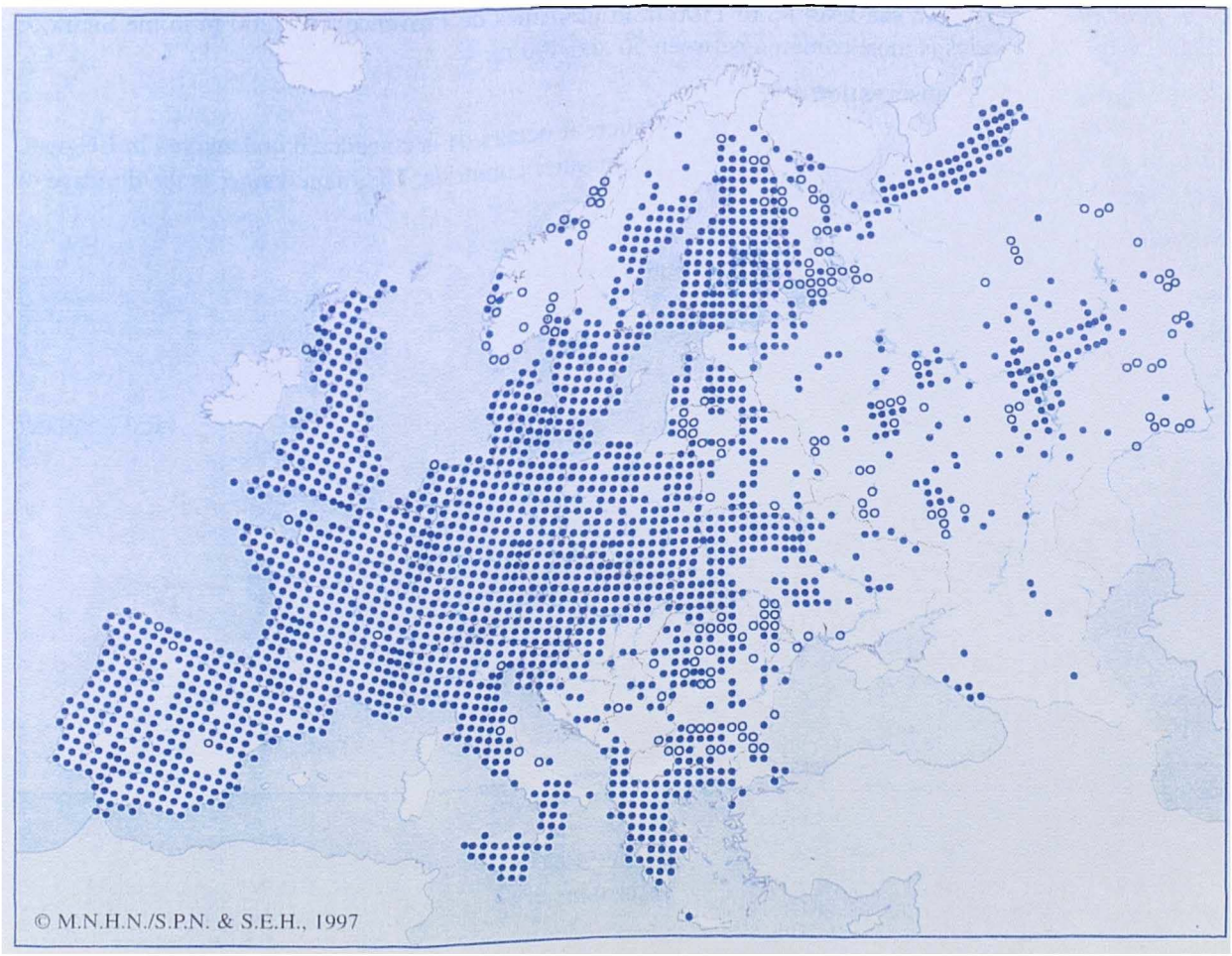


Figure 2.16: *B. bufo* and its distribution (after Gasc *et al*, 1997).

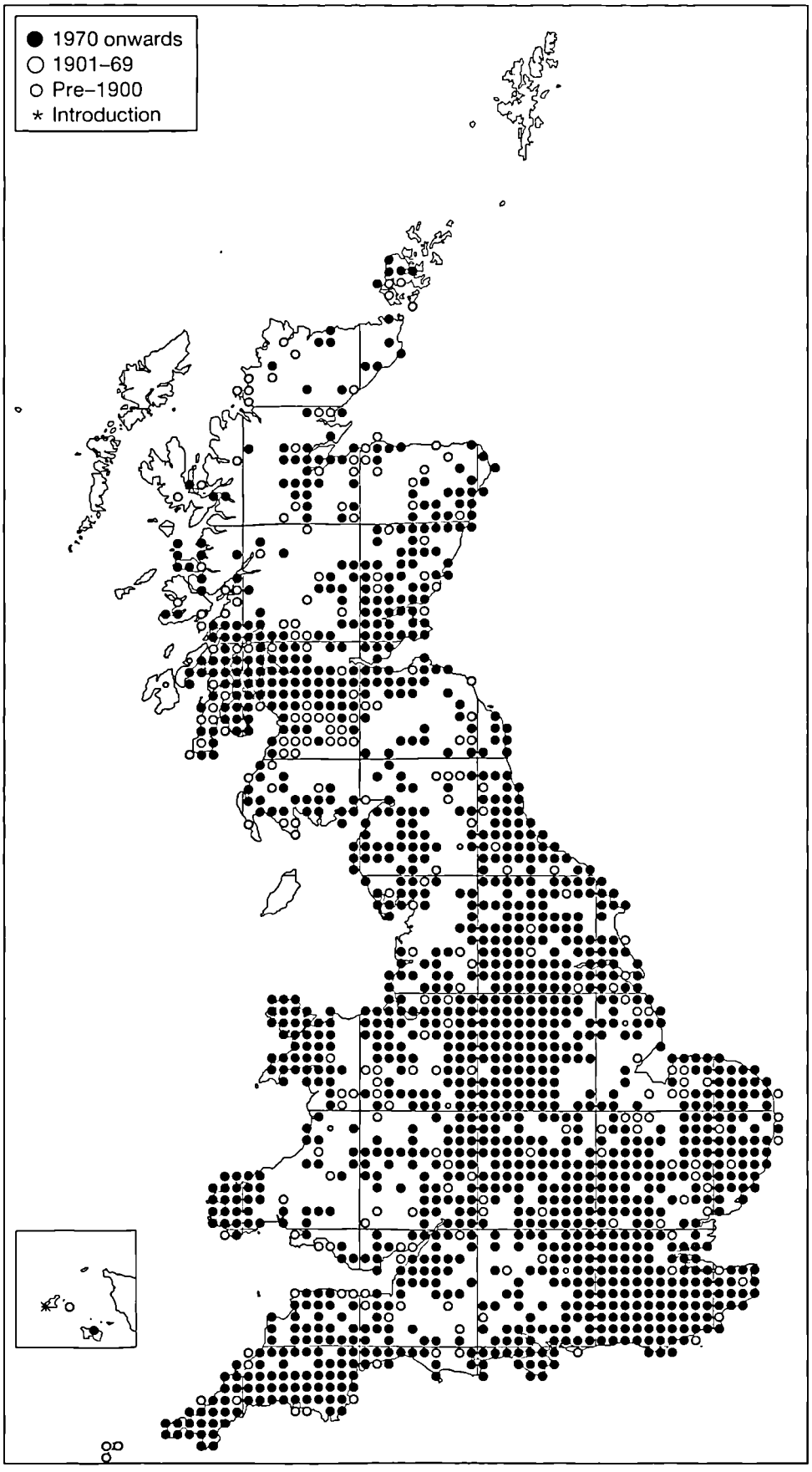


Figure 2.17: Distribution of *B. bufo* in Britain (after Arnold, 1995).

vineyards, tilled lands, open mines, building sites and a variety of unshaded terrains throughout its continental range (Beebee, 1979). In Central Europe, it is associated with industrial wasteland 'ruderal sites' (Necas *et al*, 1997), and in the Netherlands it is a rapid colonist of newly exposed reclaimed land (Boomsma and Arntzen, 1985). It burrows in sand and loose soils where it hibernates during the winter. It reaches altitudes of around 1,700m in Spain and possibly 2,600m in the Pyrenées, and around 500m in Central Europe (Arnold and Burton, 1978; Necas *et al*, 1997), but is strictly limited to low altitudes (<100m) in Britain (Beebee, 1979).

Breeding takes place in shallow ponds, such as dune slacks and brackish pools, devoid of fish and predatory invertebrates. However, the populations found in Kerry, southwest Ireland, breed around the margins of large freshwater loughs. In Denmark, some islands are inhabited by natterjacks which breed in brackish rock pools (Johnsen, 1946), and it can breed in salinities of up to 0.4% (Beebee, 1979). Eggs are laid in strings in shallow water, close to pond edges. *B. calamita* often breeds in ephemeral ponds which dry out well before the young metamorphose, and population dynamics may undergo drastic fluctuations. It is also known to abandon established breeding pools suddenly in search of others (Arnold and Burton, 1978). Beebee (1979) noted that it has a remarkably fast reproductive cycle, developing from egg to toadlet in as little as four weeks, and becoming mature in two years.

B. calamita is also adept at rapidly colonising areas of new habitat which become available, and has been termed a 'pioneer-opportunist' (Boomsma and Arntzen, 1985). It is often displaced after a few years by 'competitively superior anurans', and is sensitive to habitat change (Beebee, 1997a). The development of *B. calamita* tadpoles may be retarded by the presence of *B. bufo* tadpoles (Beebee and Beebee, 1977; Beebee pers. comm., 1997), as *Prototheca* algae, concentrated in the droppings of *B. bufo* tadpoles, is attractive to *B. calamita* tadpoles but is not nutritious. For breeding, *B. calamita* requires water temperatures of around 18-22 ^{o}C, and on average, its optimum requirements are 3^{o}C higher than those for *B. bufo* (Beebee, 1979).

B. calamita's distribution extends from Iberia and France, in a swathe northeastwards, around the Alps, across central and eastern Europe, to Belorussia and western Russia (Arnold and Burton, 1978; Gasc *et al*, 1997). The northern limit is around the Gulf of Riga, some Baltic islands and southern Scandinavia (Boulenger, 1897-8). Boulenger (1897-8) noted that, though *B. bufo* is absent from many islands, *B. calamita* is found on most of the islands within its range.

B. calamita has a scattered distribution in Britain, mainly around the coast of northwest England and southwest Scotland, but also in heaths and dunes of the south and east. It was historically more widespread, and local rather than rare (Boulenger, 1897-8; Beebee, 1978). Habitat loss and fragmentation is likely to have been the biggest factor in its decline, particularly as agriculture has expanded, heaths have been allowed to develop tree cover and coastal marshes have been drained (Beebee, 1977). It is now restricted to a few heaths and dune systems in the southeast of England, coastal dunes, saltmarshes and moorland in northwest England and southwest Scotland. It is often associated with sandy areas close to the sea, and is probably only able to

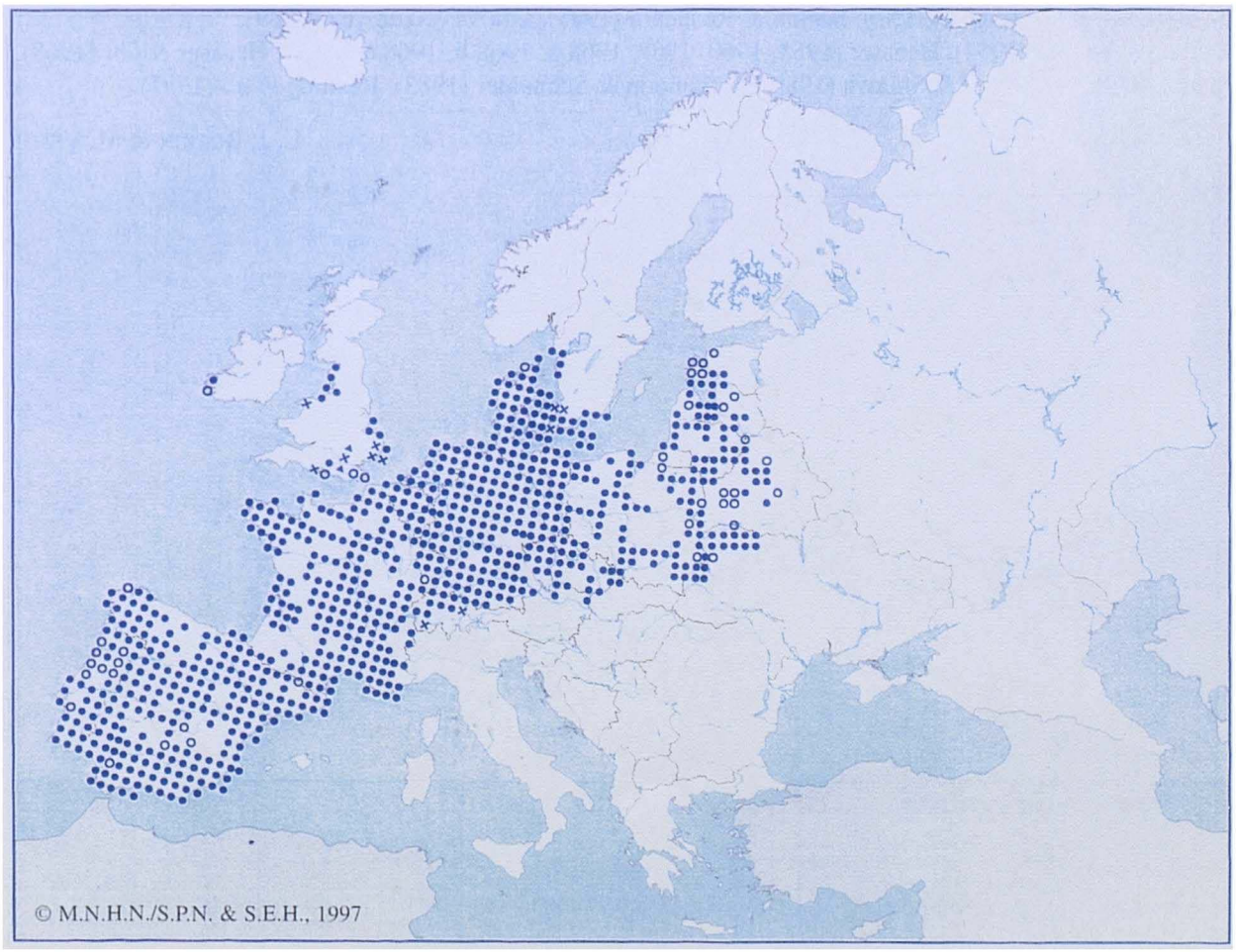


Figure 2.18: *B. calamita* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

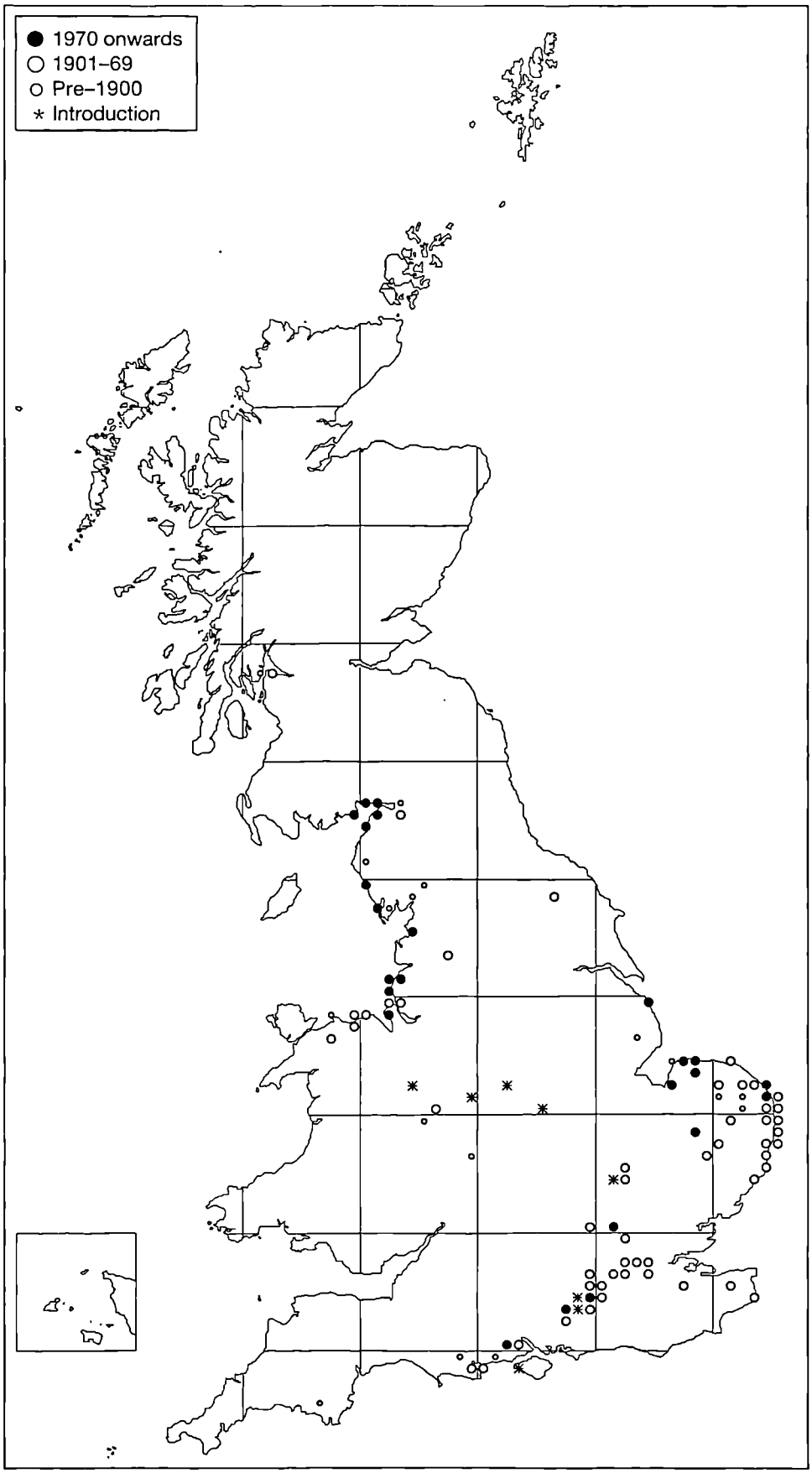


Figure 2.19: Distribution of *B. calamita* in Britain (after Arnold, 1995).

survive in the north of its range where local microclimate is favourable. This tends to be areas of open or little vegetation, on sandy soils, where insolation is received easily. The northern limit of *B. calamita* in Britain is in the Solway Firth and is most likely restricted to here by summer warmth. Across Britain and southern Ireland, *B. calamita*'s distribution matches the 15°C July isotherm (Wallén, 1970) remarkably closely.

Interestingly, Banks (1998) noted that the largest populations are in Cumbria, some of which have only been discovered in the last few years. Remarkably, *B. calamita* inhabits a wider range of habitats in Cumbria than had previously been thought, but all of these environments are characterised by unpredictability upon which *B. calamita* appears to capitalise. This seems to be key in preventing dominance by other amphibian species. Catastrophic tadpole mortality is commonplace, but in good years many thousands of tadpoles may emerge. The coastal dune and saltmarsh sites are pools of up to 1m deep, mostly but not always with a sandy substrate. The most important factor at these sites is occasional inundation with saltwater, though adjacent land is also washed by freshwater (Banks, 1998). Saltmarsh pools do not have to be as shallow and ephemeral as other sites in order to support *B. calamita*, as the saltwater inundation controls predators and competitors. *B. calamita* tadpoles resort to the shallow margins, where the water is warm enough to favour their development. The vegetation adjacent to the most successful *B. calamita* sites in Britain is kept short by grazing, and this species may have had a longstanding relationship with herbivores. Banks (1998) also reported breeding sites in river valleys, particularly in oxbows and flooded pools blocked by shingle banks. Once again, these are dynamic sites are characterised by unpredictability.

Beebee (1978) suggested that formerly, the wider distribution of undisturbed, unforested landscapes (grasslands and heaths) would probably have been more suitable to *B. calamita* than today's agricultural landscapes. He also noted that as recently as the last century, natterjacks lived in some inland areas in Britain, on land other than heathland. Gadow (1904) described *B. calamita* from inland sites in Cambridgeshire where it is now extinct. Significantly, it had a much wider distribution only fifty years ago (Taylor, 1948), yet this had contracted markedly within fifteen years (Taylor, 1963). Nevertheless, there is no evidence in support of Beebee's (1978) contention that *B. calamita* was widely distributed across tracts of land connecting populations in the northwest with those in the south.

There are also populations in Kerry, southwest Ireland, the origin of which have been the subject of debate (e.g. Fitter, 1959; Beebee, 1984; Gleed-Owen, 1997c). Fitter (1959) believed that suggestions of human introduction through the unloading of sand from ships' ballast were unreasonable. He also argued that historical records of a 'frog' near Waterford between 1184 and 1187, and later in 1630, might refer to a now-extinct population of *B. calamita*.

It is generally agreed that *B. calamita* was restricted to Iberian refugia during Pleistocene glaciations (Beebee, 1997a). Fossil remains of *B. calamita* have been recorded from a number of sites in the British Isles. Records for the species have been given from Boxgrove, Selsey,

Whitemoor Channel, Cow Cave, Ightham, Creag nan Uamh, Barclodiad y Gawres and Carrowmore (Newton, 1917; Pumphrey, 1956; Ove and Persson, 1980; Holman, 1985; 1988; 1992a; 1992d; Holman and Stuart, 1991). The material from Whitemoor Channel was incorrectly identified (Gleed-Owen, 1997a), and the record from Creag nan Uamh is doubtful and probably also mistaken (see Chapter 6). The records of *B. calamita* from Boxgrove, Cow Cave and Ightham were correctly identified, but the current author is less certain about records from Selsey.

Bufo viridis Laurenti 1768 **Green toad**

A robust toad, *B. viridis* attains up to 100mm in length, with females being largest. It is similar in many ways, and closely related, to *B. calamita* (Arnold and Burton, 1978; Beebee, 1979). Its dorsal pattern is a usually pale background with vivid green marbled markings. It is nocturnal, but may sometimes forage in the day. In Europe, it is generally associated with lowlands habitats, living in similarly dry sandy habitats to *B. calamita*, and often in large numbers in the south (Arnold and Burton, 1978). It can also breed in brackish pools (Johnsen, 1946). It is sympatric with *B. calamita* in Poland, Germany, Denmark and southern Sweden (Beebee, 1979; Gislén and Kauri, 1959; Johnsen, 1946), and hybridisation is well documented between the two species. *B. viridis* is also associated with human environments (Arnold and Burton, 1978), and, unlike *B. calamita*, is not bound to specific types of breeding sites (Roth, 1997).

B. viridis has a mainly eastern distribution (Gasc *et al*, 1997) and is seen as the eastern counterpart of *B. calamita* (Ovenden *et al*, 1979). It is not clear whether climatic controls, or merely competition, are the main reason for their separate distributions. It is found from Italy and the Balkans, across central Europe to southern Sweden, and eastwards across much of Russia (Arnold and Burton, 1978; Gasc *et al*, 1997). Gaps in its distribution in eastern countries may be due to a lack of recording rather than a true absence (Roth, 1997). It is also found most Mediterranean islands, from Crete to the Balearics, but there is evidence that at least the Balearic occurrences may be due to introduction by Bronze Age people (Roth, 1997).

It is not present in Britain, but is found in parts of Denmark and southern Sweden around the North Sea. It has not been recorded as a British fossil, but could potentially have been a Pleistocene colonist.

Family: Hylidae Gray 1825

Subfamily: Hylinae Gray 1825

Most of the Hylidae are arboreal, and possess flat, rounded toe pads used for climbing trees and bushes (Duellman and Trueb, 1986). These two European tree frogs are very similar and have ranges that are mainly mutually exclusive. Both species are considered here.

Hyla arborea (Linnaeus 1758) **Common tree frog**

H. arborea is a distinctive frog, with long, slender limbs and smooth skin. Adults usually reach

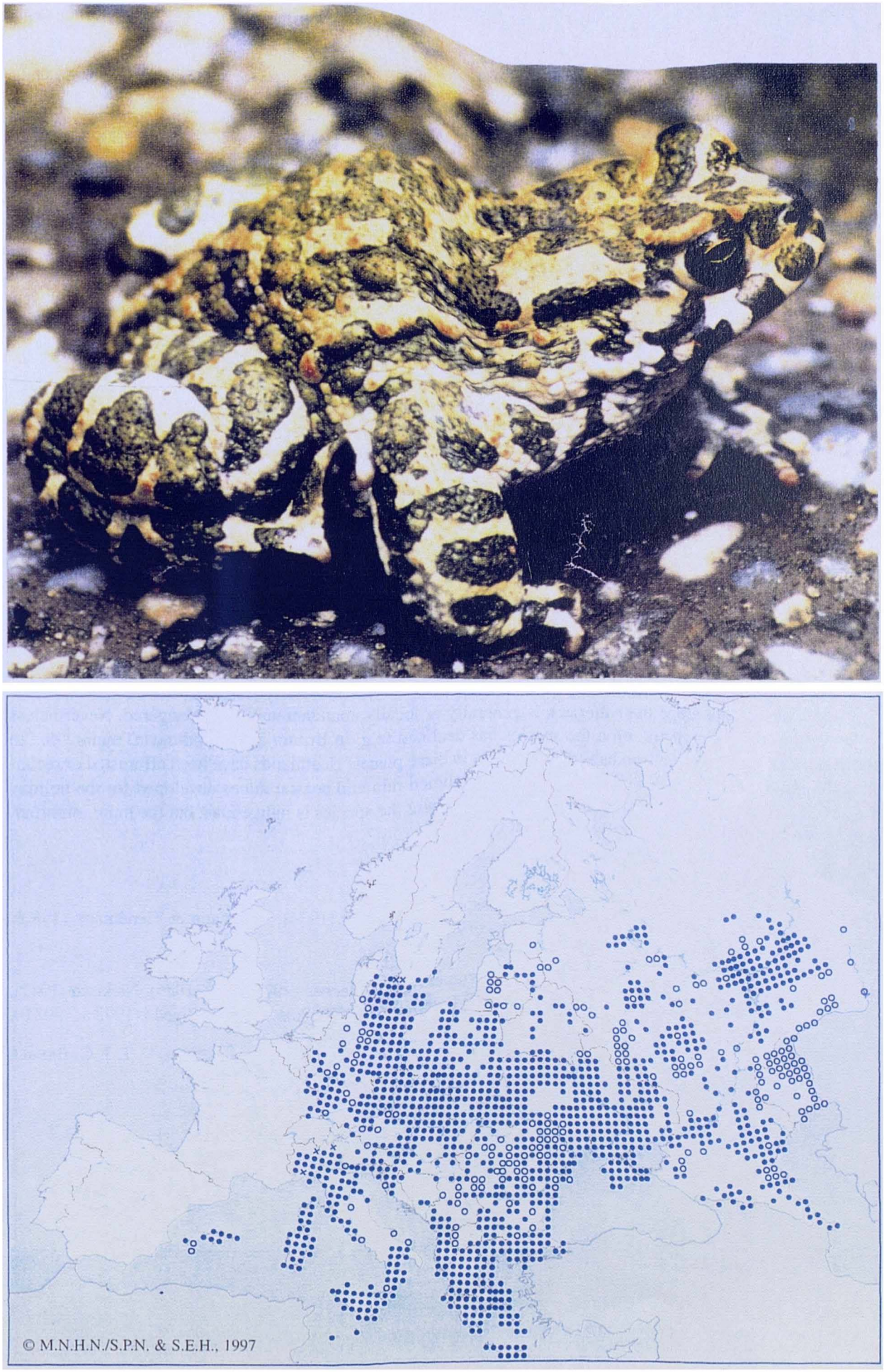


Figure 2.20: *B. viridis* and its distribution (after Gasc *et al*, 1997).

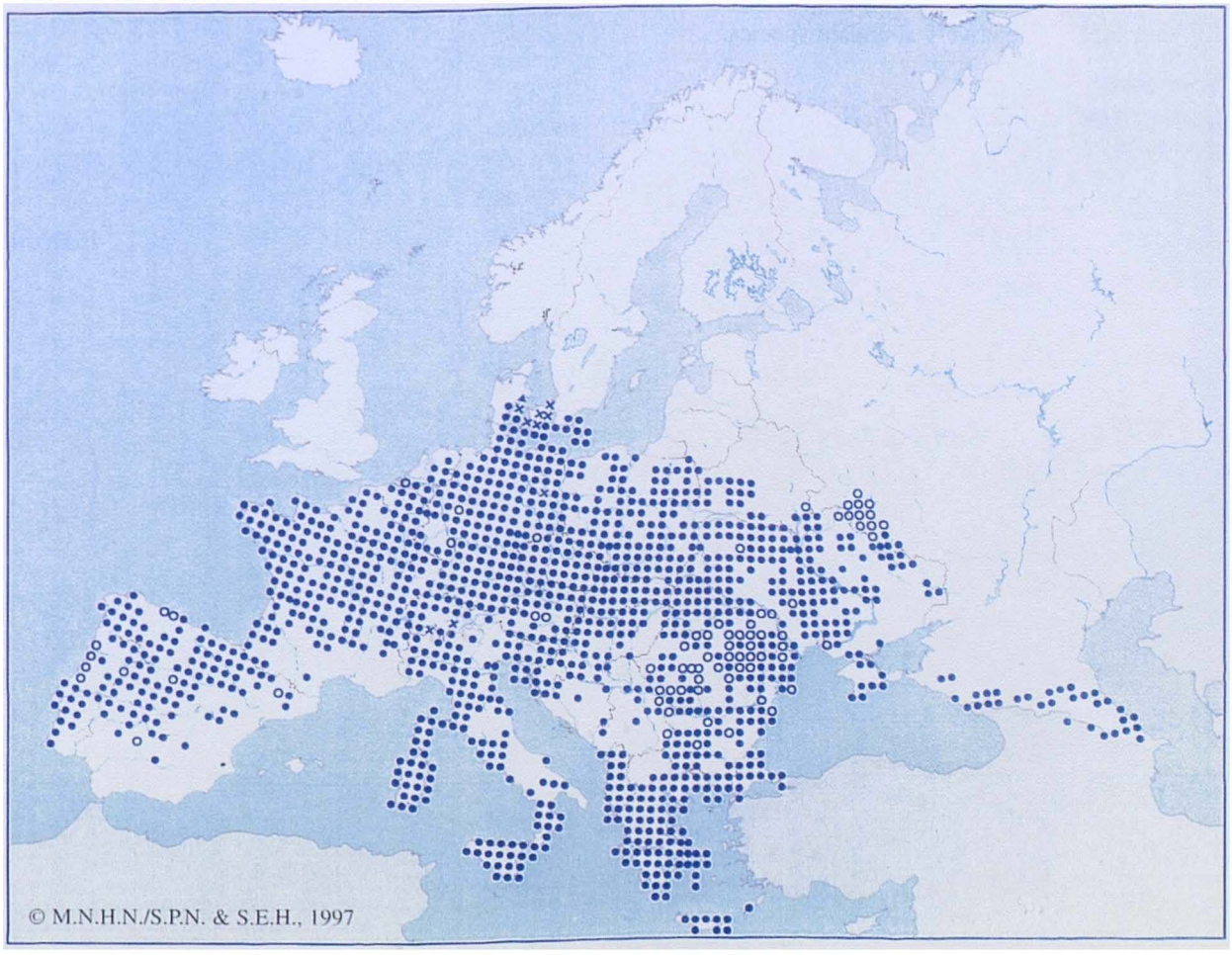


Figure 2.21: *H. arborea* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

around 50mm in length. It is variable in colour: normally a bright green, although females may be a duller brown, with a dark stripe along each side of the head and body. In northern Europe, it is a lowland species seldom reaching above 500m. Its altitudinal distribution becomes greater further south, reaching c.800m in the Alps, 1900m in Spain and 2,300m in Bulgaria (Stumpel, 1997).

It is mostly nocturnal, living in well-vegetated places, especially in waterside bushes, trees and reed beds (Arnold and Burton, 1978). It climbs extensively, though young animals tend to stay low in herbage, and feeds by leaping at passing insects (Ovenden *et al*, 1979). During the breeding season, *H. arborea* gathers in ponds in large numbers, creating a loud nocturnal chorus (Ovenden *et al*, 1979). Breeding takes place in deep pools of clear, richly-vegetated water (Boulenger, 1897-8). Metamorphosis takes place especially after rain, and may have originated many stories of 'raining frogs' (Boulenger, 1897-8).

H. arborea has a disjunct range, which is almost totally mutually exclusive with that of *H. meridionalis*. It is absent from parts of southern France, but is distributed in suitable habitats over most of Europe, and into southwest Asia. It reaches north to the Baltic coast, including Denmark and southern Sweden, and into Belorussia and Ukraine (Arnold and Burton, 1978; Gasc *et al*, 1997). It reaches 55°N in Denmark and southernmost Sweden, declining southeastwards from Poland to Ukraine (Gasc *et al*, 1997), and its northern distribution is closely determined by the 16°C July isotherm (Stumpel, 1997).

It is not native to Britain, though introductions have been successful on the Isle of Wight. A single bone of '*Hyla* sp' was recorded from Cudmore Grove (Holman *et al*, 1990), and unspecified *H. arborea* remains were recorded from Barnham (Ashton *et al*, 1994). Owing to the close similarities between the two European *Hyla* species, the record of '*H. meridionalis*' from Itteringham (Holman, 1992b) should be considered as potentially belonging to *H. arborea*.

Hyla meridionalis Boettger 1874 **Stripeless tree frog**

This species is a close relative of *H. arborea* and differs mainly in its markings, as the name suggests. It is otherwise similarly long-legged, smooth-skinned and adept at climbing waterside vegetation. Adults can reach around 50mm and may be bright grey or occasionally blue, but with a dark stripe only along the side of the head (Arnold and Burton, 1978). *H. meridionalis* occupies similar habitats to *H. arborea*, but where their ranges overlap in France, it is usually found at lower altitudes, though occasionally it reaches over 1,000m (Arnold and Burton, 1978; García París, 1997).

H. meridionalis has a disjunct range, much of it mutually exclusive with that of *H. arborea*. One part covers most of southern Iberia; the other European group covers northwestern Italy southern and western France, reaching north to the Loire Valley. Within these areas, populations are not continuous and some populations are isolated (García París, 1997). It also extends into Cataluña, and is found in the Balearic Islands (Arnold and Burton, 1978; García París, 1997; Gasc *et al*, 1997). Its range also extends into northwest Africa (Bons and Geniez, 1996). The northern

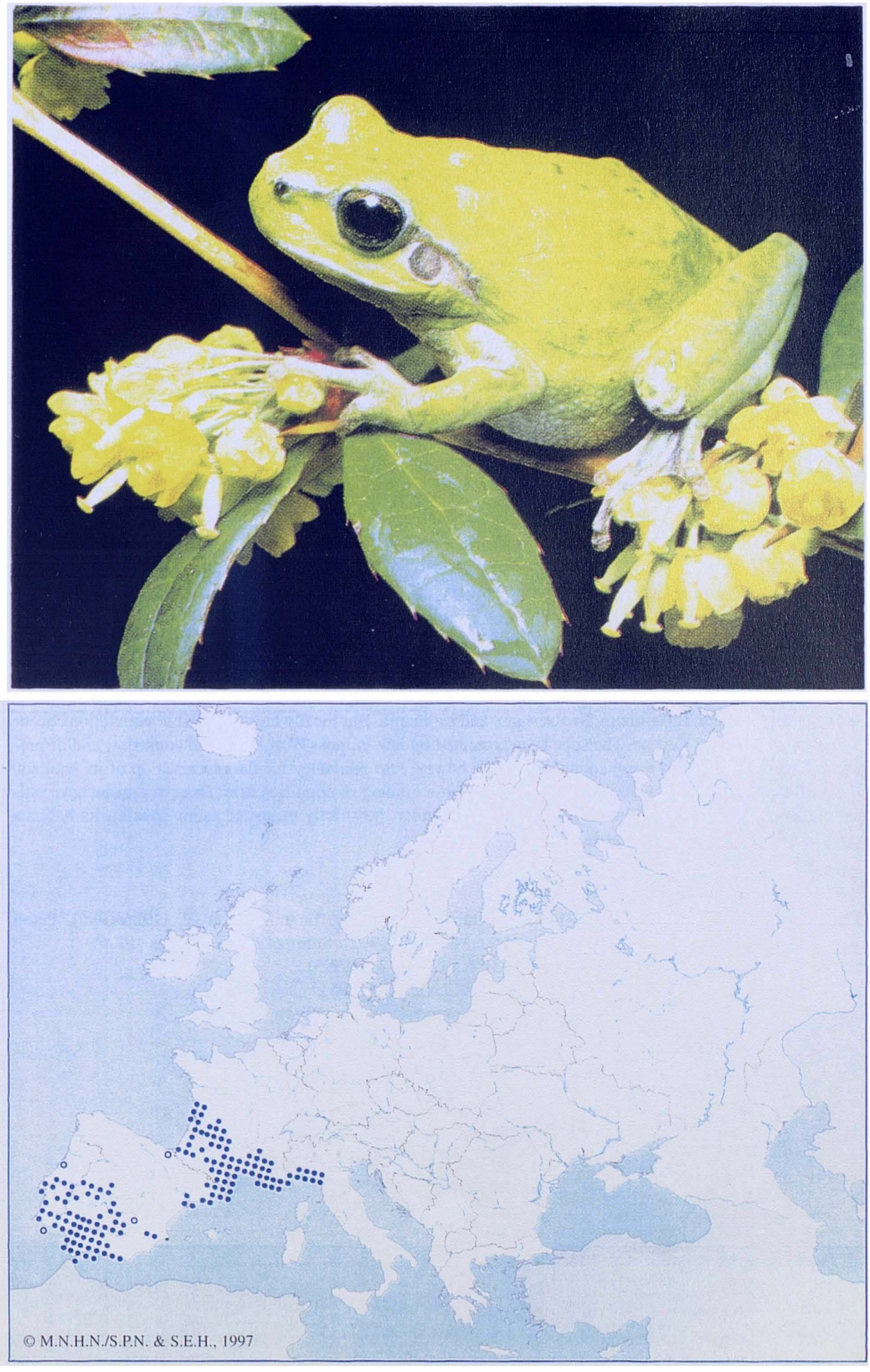


Figure 2.22: *H. meridionalis* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

limits of its range are uncertain, but appear to be restricted by cold and dry regions of the Iberian Central Plateau (García París, 1997).

H. meridionalis was recorded from Itteringham (Holman, 1992b), but this identification should be viewed with some caution as other workers (Sanchiz and Mlynarski, 1979) have been unable to separate fossil material of *H. arborea* and *meridionalis*. *H. arborea* would be a more likely British colonist as it ranges much closer. If correctly identified, this is the most southerly species apparently recorded from the Pleistocene of the British Isles. It is also the most southerly species considered here.

Family: Ranidae Gray 1825

Subfamily: Raninae Gray 1825

The Ranidae (typical frogs) are distributed globally, except in some arctic regions, northeast Asia, and Australasia. They are very variable in size and habits, though most are semi-aquatic and have long legs with webbed feet (Duellman and Trueb, 1986). The genus *Rana* is represented across the western Palaearctic sub-region (Boulenger, 1897-8). They are agile frogs, capable of long leaps, and are powerful swimmers (Arnold and Burton, 1978). During the breeding season, they gather in large numbers, in ponds where mating takes place. The European species are separated into two groups: the brown frogs and green frogs. Females lay clumps of spawn often containing around 2,000 eggs, and up to 10,000 in a mature green frog (Arnold and Burton, 1978).

Brown frog group

The European species of brown frog are much more terrestrial and less gregarious than the green frogs, and males lack vocal sacs in the cheeks (Arnold and Burton, 1978). Their snout is generally less pointed, and the eyes are further apart than green frogs. Three species have distributions in northern Europe and will be considered here. Only one of these (*R. temporaria*) is native to Britain today.

Rana temporaria Linnaeus 1758 Common frog

Adult *R. temporaria* can reach 100mm, but are usually smaller. This is the world's most widespread frog, and in many parts of its range, the most abundant (Arnold and Burton, 1978). Its colour is very variable, ranging from grey to olive-brown or yellowish above, with darker blotches and often a scattering of black spots. The underside is pale, or can be a brighter yellow or orange, often mottled or marbled with darker markings. Males have very strong forelimbs, and develop large black nuptial pads on the hands, during the breeding season. It is largely a terrestrial animal, and is generally only found in water when breeding. It is widespread in many different habitats, throughout its range, wherever there is moist ground (Necas *et al*, 1997). It is found around glacial meltwater streams in the French Alps and in Scandinavia, and is the most cold-tolerant species of the European herpetofauna. At its northern limit, it is only absent in areas of permafrost (Arnold

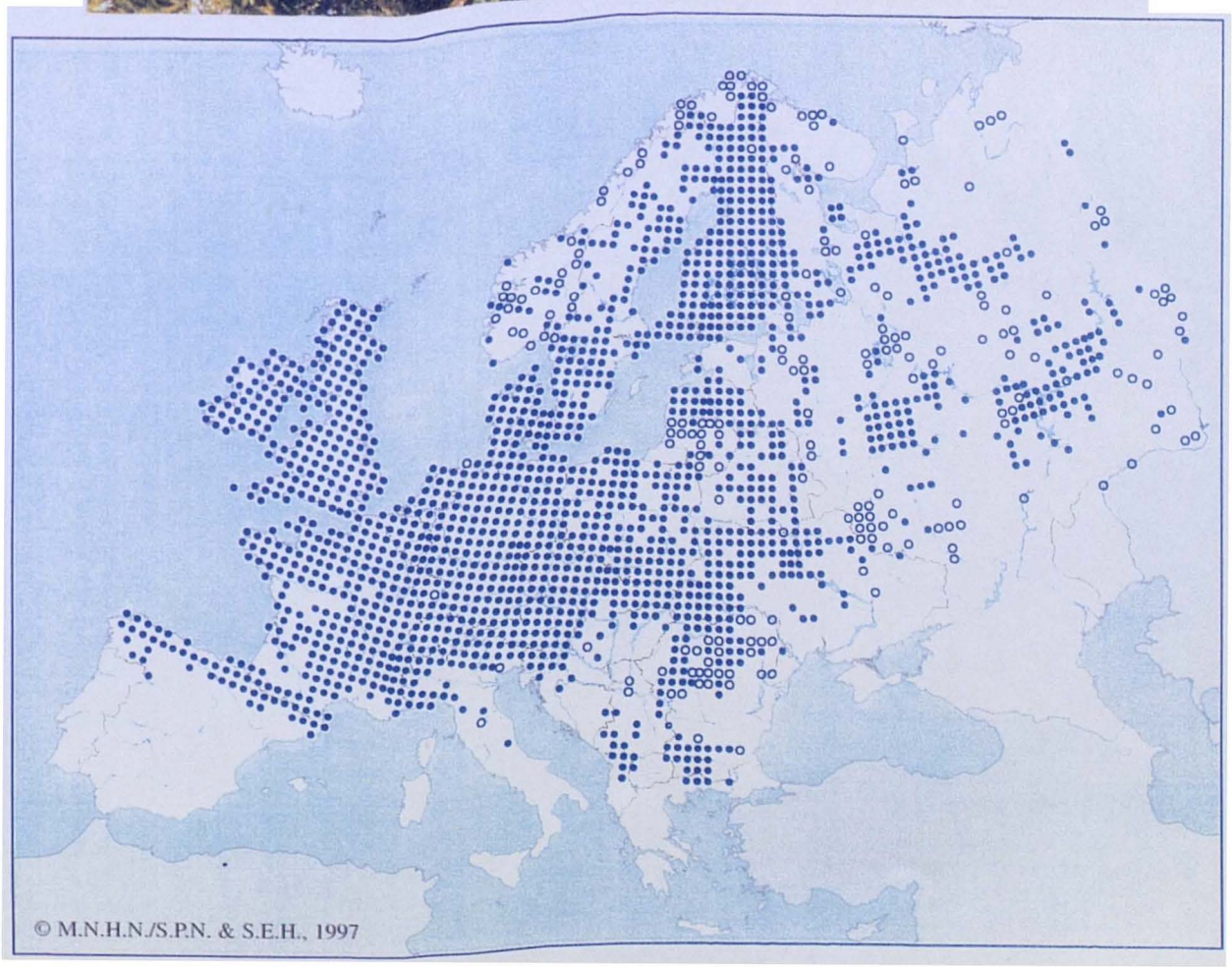


Figure 2.23: *R. temporaria* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

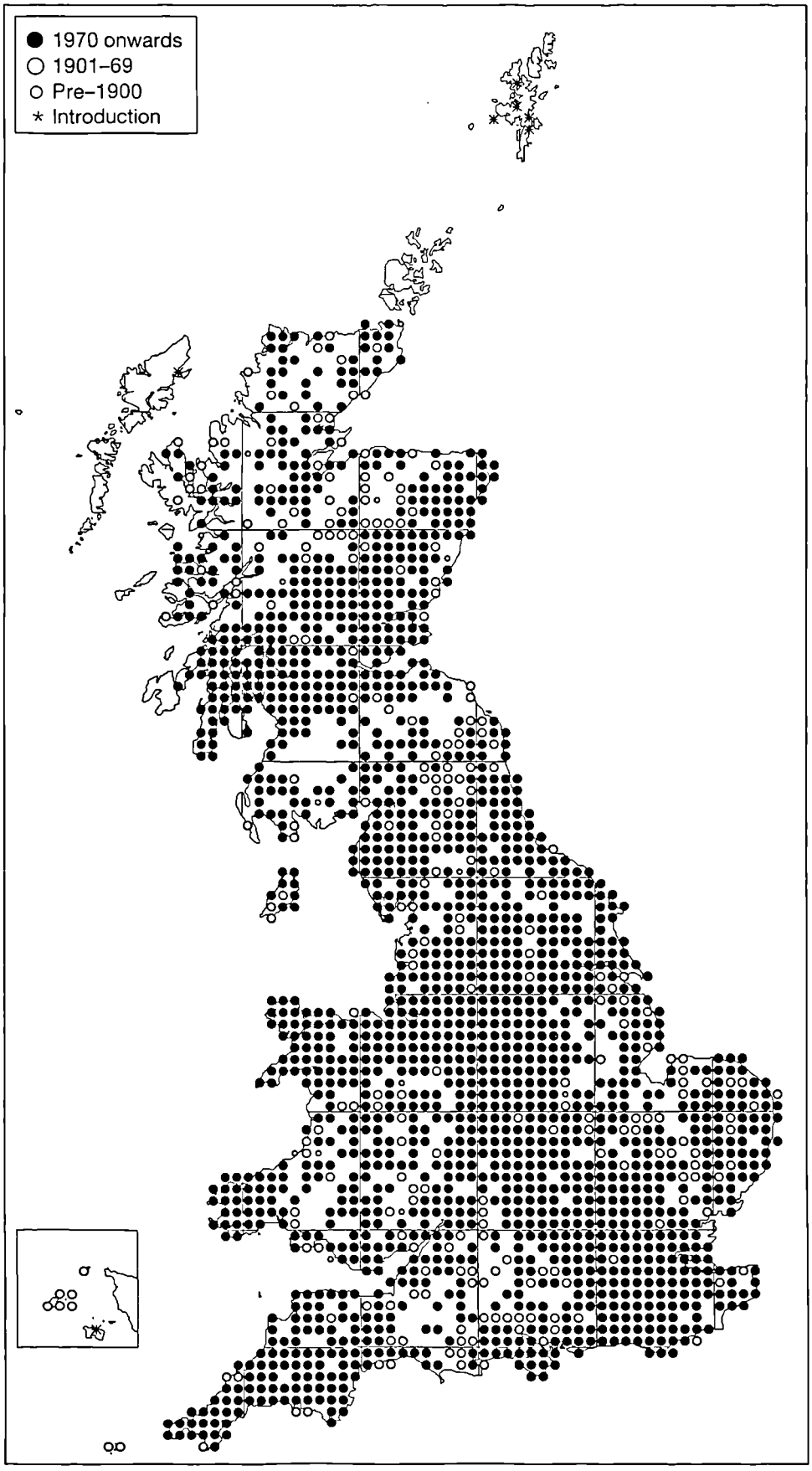


Figure 2.24: Distribution of *R. temporaria* in Britain (after Arnold, 1995).

and Burton, 1978). The spring breeding season begins earlier than most other European anurans, and clumps of spawn are laid in any shallow water, including the shallowest of pools and marshy depressions, which often dry up before summer. Spawn often dries out, is killed by fungus, or eaten by other animals, and adults appear to show no foresight in their selection of spawning places.

The distribution of the *R. temporaria* is the most extensive of all European frogs, ranging across most of Europe, except the south. It ranges east to the Urals, but here is becomes less common and is largely replaced by *R. arvalis* (Grossenbacher, 1997b). It stretches north across all of Scandinavia, reaching the Arctic coast. It is absent from most of Iberia, but is present in a disjunct band from Galicia to the Pyrenées (Gasc *et al*, 1997). Elsewhere, its southern limit reaches into northern Italy, and the northern Balkans, but moves northeast into Ukraine and Russia (Arnold and Burton, 1978; Gasc *et al*, 1997). It is widespread throughout Britain and Ireland, and has been recorded as a British fossil on many occasions. *R. temporaria* may well have been present in southern Britain during glacial periods, and could have been the earliest amphibian coloniser of freshly deglaciated areas. As it is the least thermophilous amphibian species considered here, it can offer only very limited palaeoenvironmental information. It has been suggested that *R. temporaria* may have been introduced to Ireland during historical times, because of its reported absence in Mediaeval literature (Wilson, 1983). Grossenbacher (1997b) claimed that it was introduced 300 years ago. Nevertheless, its previous absence from Ireland would be anomalous and difficult to explain. Fitter (1959) arrived at this conclusion and argued that *R. temporaria* was probably already native in the west of Ireland, where it is more common today, but was introduced on several occasions in the east. There are historical records between 1184 and 1187, and in 1630, of a 'frog' found near Waterford in the east. Fitter (1959) suggested that these records could have been either *R. temporaria* or *B. calamita*.

R. temporaria has been the most commonly identified species from the British Quaternary. Its bones have been identified from West Runton, Westbury-sub-Mendip, Boxgrove, Purfleet, Bakers Hole Pit, Swanton Morley, Itteringham, Nazeing, Tornewton Cave, Upton Warren, Cow Cave, Ightham, Whitemoor Channel, Dog holes, Creag nan Uamh, Happaway Cave, Netteswell, Bathford, Barclodiad y Gawres, Tiddington and Repton (Newton, 1882a; 1882b; 1894; 1917; Allison *et al*, 1952; Pumphrey, 1956; Stuart, 1982; Holman, 1985; 1987b; 1987b; 1987c; 1988; 1989; 1990; 1992a; 1992c; 1993a; 1995a; Holman and Clayden, 1988; Holman *et al*, 1988; Hallock *et al*, 1990; Raxworthy *et al*, 1990; Holman and Stuart, 1991).

Rana arvalis Nilsson, 1842 **Moor frog**

R. arvalis can reach up to around 80 mm. It has significantly shorter legs than *R. temporaria*, and tends to have a striped dorsal pattern, but otherwise is similar in appearance. A separate subspecies, *R. a. wolterstorfii*, is recognised from southern parts of its range, having longer legs and a more slender body (Arnold and Burton, 1978). *R. arvalis* is found in a range of

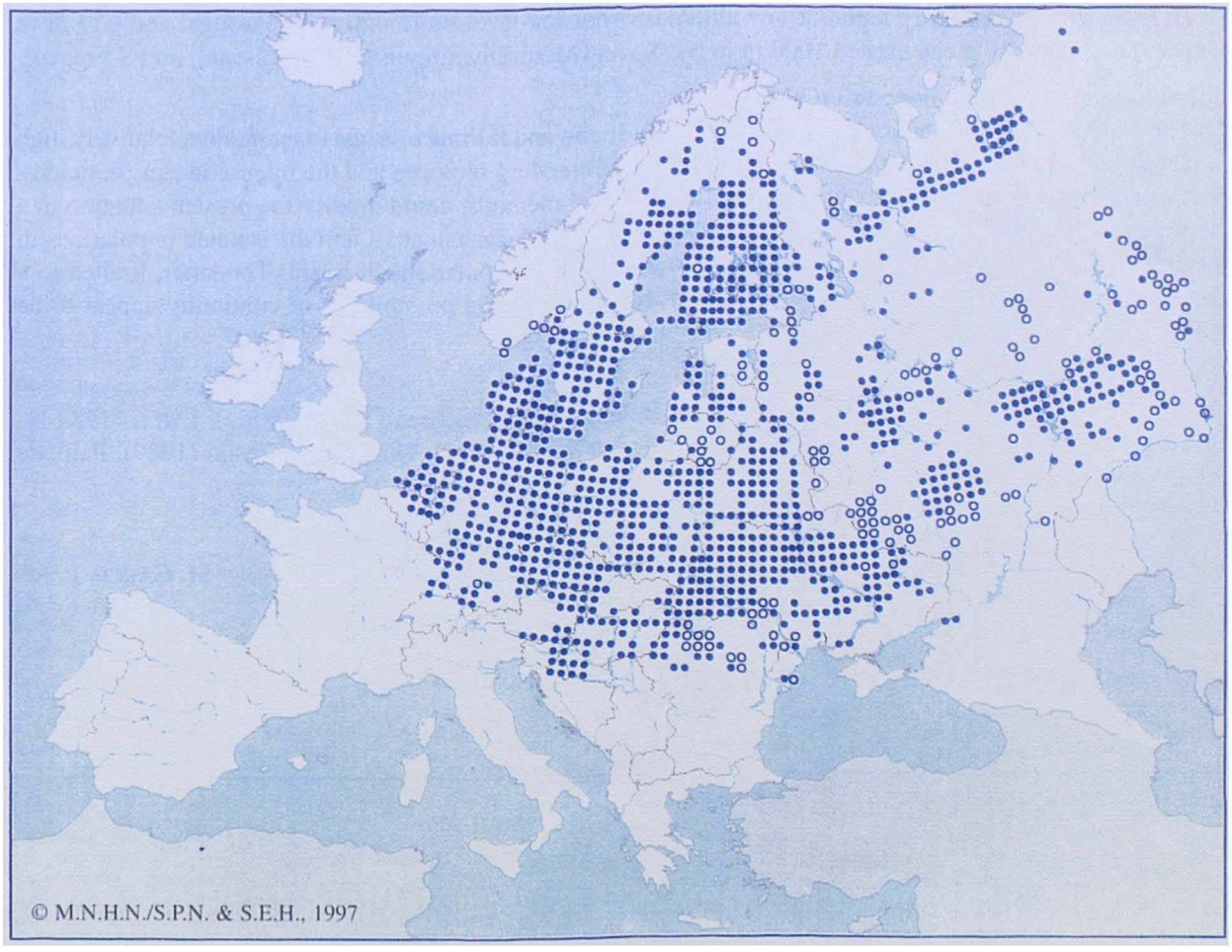


Figure 2.25: *R. arvalis* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

environments, including damp fields, meadows, marshes, fens and sphagnum bogs. It is usually associated with wetter habitats than *R. temporaria*, in areas where both species are found, though it is not more aquatic. Necas *et al* (1997) reported that it is strictly associated with very humid environments, and apparently becomes more associated with woodlands in the south of its range, except at higher altitudes. In western central Asia, it is primarily associated with deciduous, mixed and light coniferous forests, extending into marshes and floodplains (Ishchenko, 1997). Breeding is often in temporary pools, within the usual habitats. Like *R. temporaria*, it often lays its eggs in shallow puddles where there is no chance of the young surviving (Boulenger, 1897-9; Arnold and Burton, 1978). *R. arvalis* prefers acidic water bodies of pH 5.0-6.0 (Ishchenko, 1997), and is considered to be an indicator of the biological health of unpolluted moorland pools (Corbett, 1989).

Besides *R. temporaria*, *R. arvalis* has the most northerly distribution of the European frogs. Its range is essentially eastern, reaching 69°N in northern Scandinavia and the Barents Sea coast in Russia (Ischchenko, 1997), though Boulenger (1897-8) claimed that it did not reach this far north. Its southern limit crosses from northeast France, across the Alps and the Carpathians, to the northern Black Sea coast (Arnold and Burton, 1978; Gasc *et al*, 1997). It is absent from southwest and southern Europe, just reaching the head of the Adriatic. Eastwards, *R. arvalis* reaches Russia and Siberia. It is absent from the British Isles, and also the western side of Scandinavia, but is present around the whole North Sea coast of mainland Europe (Arnold and Burton, 1978). Boulenger (1897-8) suggested that its range represents a great reduction from a formerly more widespread occurrence. In many western areas, he noted that its distribution is broken and 'spot-like', and its restriction to wetter areas such as *Sphagnum* bogs reflects its true preferences. *R. arvalis* is tied closely with continental climates. In the north, it is absent from Scandinavia, and in the south, it is only found in eastern parts of Europe, where winters are very cold (Martínez Rica, 1997).

Pleistocene fossil remains of *R. arvalis* have been found regularly from sites in southeast England. It is known from interglacial deposits at West Runton, Sugworth, Boxgrove, Barnham, Purfleet, Cudmore Grove, Swanton Morley and Shropham (Ashton *et al*, 1994; Holman, 1987a; 1987c; 1989; 1992a; Holman and Clayden, 1988; 1990; Holman *et al*, 1988; 1990). There are no cold-stage records for *R. arvalis*, though it could probably have survived, in southern Britain at least, during some 'cooler' parts of the Pleistocene. Remains of *Rana* cf. *arvalis/dalmatina* have recently been identified from Holocene (Middle Saxon) Fenland sites at Gosberton (Lincolnshire) and Terrington St. Clement (Norfolk) (Gleed-Owen and Joslin, 1996; Gleed-Owen, 1997c; Gleed-Owen, 1997e; see Chapters 6 and 8).

Rana dalmatina Bonaparte, 1840 **Agile frog**

This species can reach 90mm, but is generally smaller. It is a slim, long-legged frog, with a delicate colouration, and often a slightly translucent appearance. It is usually a yellow-buff or

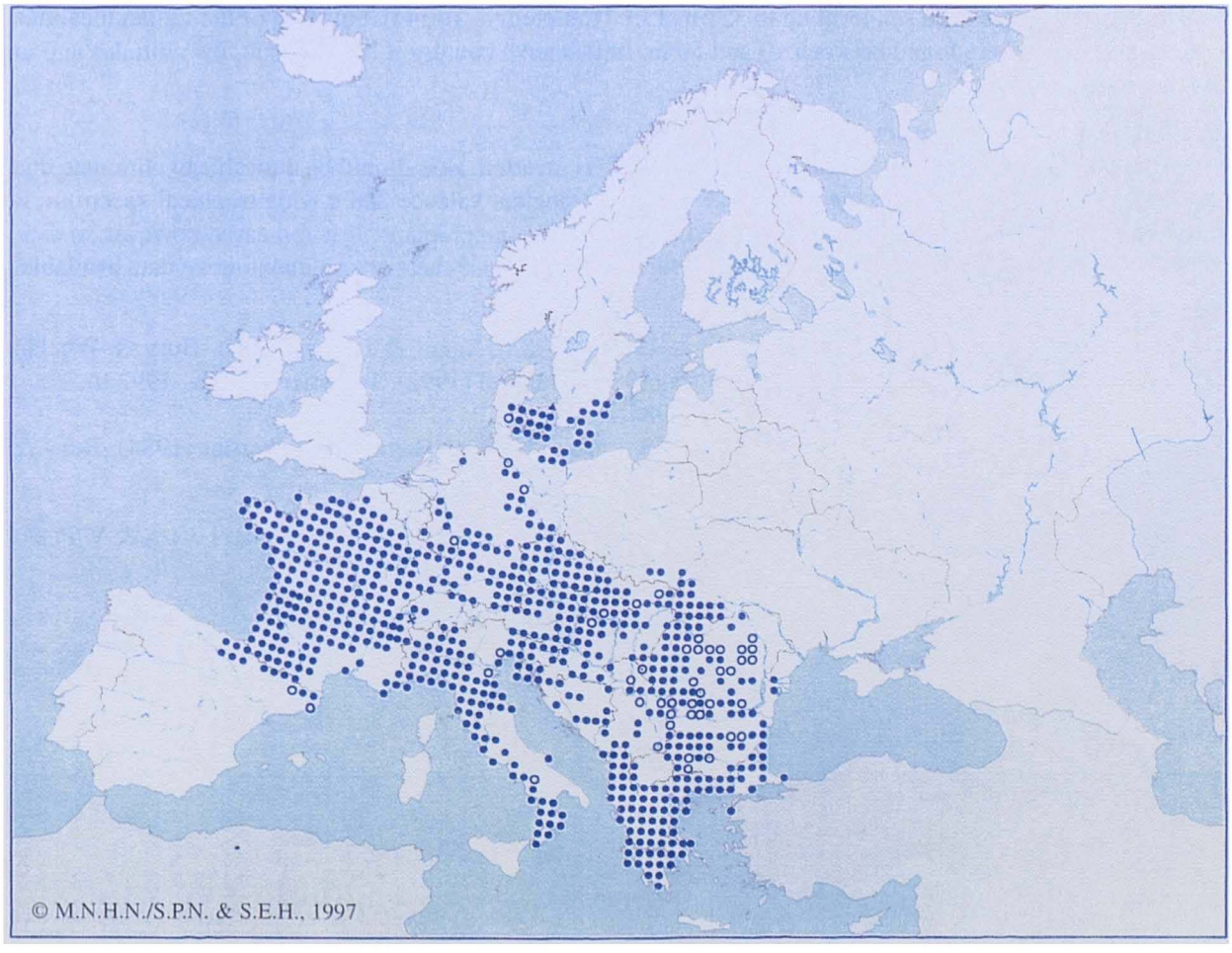


Figure 2.26: *R. dalmatina* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

inkish-brown above, with darker blotches, resembling the colour of dead leaves (Arnold and Burton, 1978). The underside is pale, with a yellow groin, and the legs are strongly banded. It is typically found in swampy meadows and light deciduous woodland (Grossenbacher, 1997c; Necas *et al*, 1997), where its colouration camouflages it well in leaf litter. In the north, *R. dalmatina* inhabits Danish beech forests, but mainly oak forests in Central Europe, and birch and chestnut forests further south (Grossenbacher, 1997c). It is extremely agile, and capable of long leaps, but is not a good swimmer. It therefore tends to be mostly terrestrial, taking to water only occasionally (Arnold and Burton, 1978). It is also known from riverine forsets, in association with oak, hornbeam, ash and lime, although outside the breeding season, it may retreat to very dry parts of the forest (Grossenbacher, 1997c).

Its distribution is in a band from the western coast of France, across central Europe, to the Black Sea coast. It is absent from Iberia except the Pyrenées, but is found throughout mainland Italy and most of Sicily, and the Balkan peninsula. It has a disjunct northern range and its distribution becomes sporadic and scattered in the north (Grossenbacher, 1997c). The limit of its continuous distribution stretches from northeast France, across southern Germany and Poland, to Romania. There are isolated occurrences throughout northern Germany, Denmark and southern Sweden, where it is present on a number of islands up to 57°N (Arnold and Burton, 1978; Gasc *et al*, 1997). Its range must have once been continuous, and has probably been reduced by habitat loss from woodland clearance, or perhaps by climatic changes. Gaps in its central European distribution can be attributed to the unsuitable climate of hilly and mountainous country (Grossenbacher, 1997c).

R. dalmatina is not found in the British Isles, but is present along the French coast of the English Channel, including the island of Jersey, and in scattered localities around the North Sea coast of southern Scandinavia. Pleistocene immigration into Britain may have been possible, providing a corridor of suitable habitat was in existence. Several possible records of *R. dalmatina* are reported in Chapter 6 and discussed in Chapter 8.

Green frog group

The green frogs are notably thermophilous and much more aquatic than the brown frogs. They have a roughly triangular head, with a pointed snout and close-set eyes. They are voracious feeders, and will attempt to eat anything that moves (Arnold and Burton, 1978). They will jump readily from the water to catch flying insects. One species, *R. esculenta*, is a hybrid of the other two species, *R.ridibunda* and *R. lessonae*. *R. esculenta* can sometimes reproduce successfully with each other, or with the parent species, to produce fertile offspring of *R. esculenta*.

Rana ridibunda Pallas 1771 **Marsh frog**

This is the largest European frog, reaching up to 150mm. It has a robust build, with relatively longer legs than *R. lessonae* or *esculenta*. Its colouration is usually dark olive or green above, with

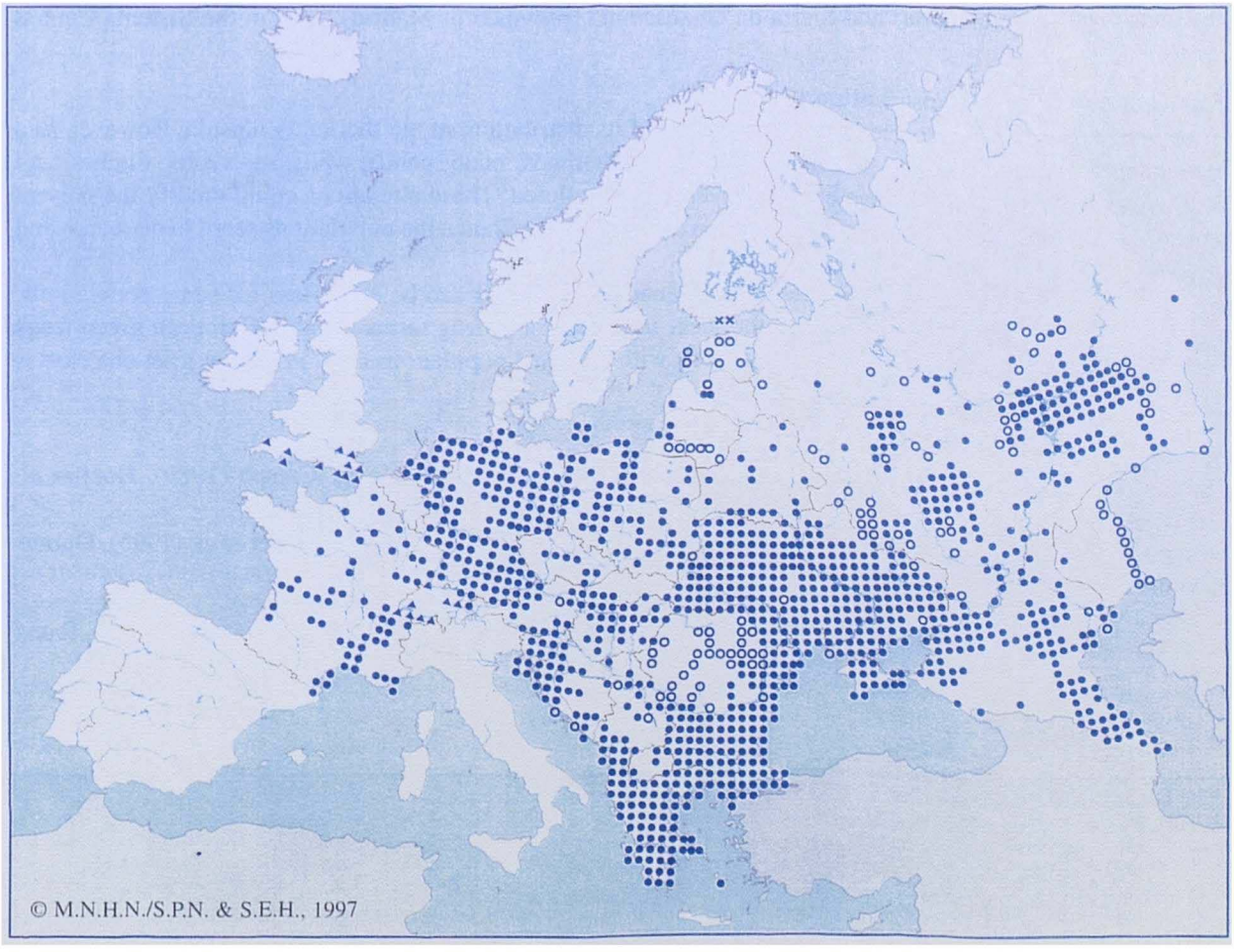


Figure 2.27: *R. ridibunda* (after Morrison, 1994) and its distribution (Gasc *et al*, 1997).

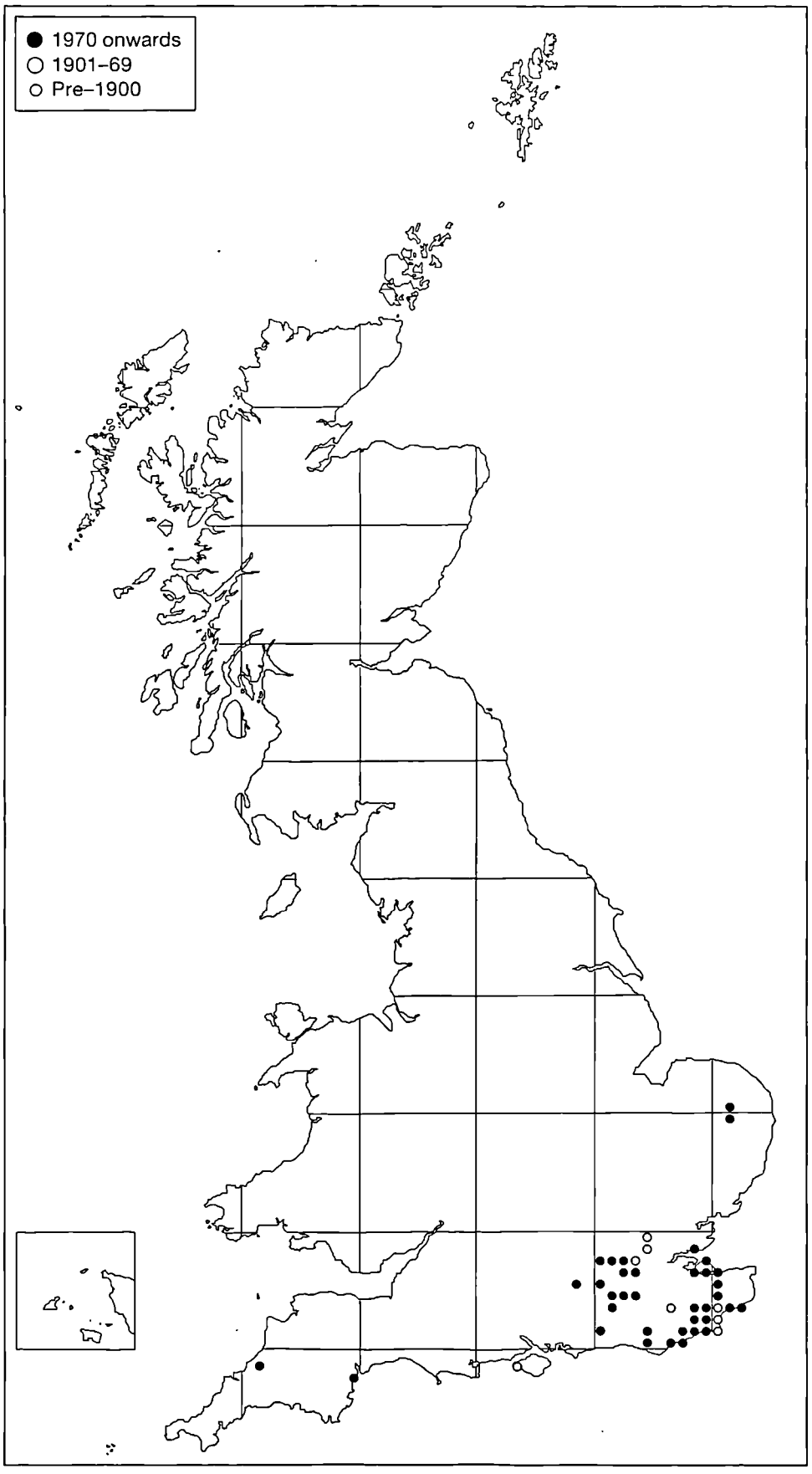


Figure 2.28: Distribution of *R. ridibunda* in Britain (after Arnold, 1995).

darker spots and markings. Its legs may be banded and its underside is pale or marbled. It is gregarious and very aquatic, spending more time in water than *R. lessonae* or *esculenta*. It is active by day, when it will attempt to eat any moving object small enough to swallow (C. Snell, pers. comm.). It occurs in all types of water bodies, including ditches and streams, particularly in southern Europe (Necas *et al*, 1997). In Central Europe, it prefers sunny, eutrophic ponds and lakes, generally over 2,000m^2 and at least 50cm deep, with rich aquatic and waterside vegetation (Günther, 1997a). Where its range overlaps with the other green frogs, it tends to be confined to large lakes and rivers (Arnold and Burton, 1978). *R. ridibunda* is thermophilous and spends much of its time basking on grass banks, lily pads, and in water weed (Arnold and Burton, 1978; Necas *et al*, 1997). They are apparently most at home where few other anurans are found, and particularly in marshland within grazed, rather than arable, areas (Frazer, 1983). During breeding, spawn is deposited in around 30cm of water, often among weed, where the secretive tadpoles become voracious carnivores. Juveniles mature rapidly, and both sexes are sexually mature within two years (Frazer, 1983).

The range of *R. ridibunda* was formerly disjunct and split into two large areas, together covering much of Europe. However, the western race has recently been recognised as a separate species, *Rana perezi* (described by García París, 1997b). As its northern range limit does not reach the Loire Valley, it will not be considered here. It is biologically very similar to *R. ridibunda.*

The range of *R. ridibunda* is essentially eastern, but its distribtuion is scattered across much of its range (Gasc *et al*, 1997). It covers much of France, the low countries, Central and Eastern Europe into Russia. It is probable that some areas, including most of the French populations are introduced (Günther, 1997a). Southwards it extends through the Balkan Peninsula, and around the Black and Caspian Seas (Arnold and Burton, 1978; Gasc *et al*, 1997; Günther, 1997a). Areas of overlap with *R. lessonae* exist in France and central Europe (Günther, 1997a; Necas *et al*, 1997), but *R. ridibunda* is absent from Italy and much of France, where it is replaced by *R. lessonae*. A population was successfully introduced into southern Italy (Arnold and Burton, 1978), therefore competition probably prevents sympatry with *R. lessonae* over a wider area. It has been suggested that the recent ranges of the green frogs are relicts of their 'maximum dispersal' during an optimum climate of the mid-Holocene Atlantic period (Böhme and Günther, 1979). Its current northern limit is about 54^{o}N in northern Germany and 57^{o}N in Lithuania, but older records reach 2-3^o further north (Gasc *et al*, 1997), and its range appears to have retracted southwards.

R. ridibunda has also been introduced to southern Britain on various occasions (Arnold and Burton, 1978) and maintains a scattered distribution in parts of southern England (Arnold, 1995). Probably the first introduction took place at two sites in Surrey in 1884 (Arnold, 1995), but an introduction on the edge of Romney Marsh (Kent), in the winter of 1934-5, has given rise to the largest population. Its spread was apparently undeterred by occasional inundations of brackish water to the Marsh, and *R. ridibunda* has since reached neighbouring areas of Kent and East Sussex (Frazer, 1983). The rate of dispersal has been estimated at half a mile a year (Menzies,

1962). Various introductions were made to the Somerset Levels and Yorkshire (Frazer, 1983), and there are persistent populations in Devon and Cornwall, and at many sites in southeast England (Arnold, 1995). In Norfolk, introduced populations of *R. ridibunda* live in oxbows and other lakes near large rivers (Buckley, 1986).

Bones of *R. ridibunda* may have been found at West Runton, Cudmore Grove and Itteringham, but only identification as '*R. ridibunda/esculenta*' has been possible (Holman *et al*, 1988; 1990; Hallock *et al*, 1990). Indeterminate green frog remains were also found at Shropham (Holman and Clayden, 1990).

Rana lessonae Camerano 1883 **Pool frog**

R. lessonae are smaller than *R. ridibunda*, usually up to around 90mm in length, but are otherwise similar in appearance. It is usually green and brown above, with a yellow-green vertebral stripe, but breeding males may be a pale green colour (Arnold and Burton, 1978). Its legs are noticeably shorter than *R. ridibunda* and *esculenta*. *R. lessonae* is generally found in relatively small water bodies, often less than $100m^2$ (Günther, 1997b), but occasionally in larger ponds and lakes (Arnold and Burton, 1978). Marshy pools and fens are typical habitats, often with neighbouring swampy meadows and waterlogged woodland (Necas *et al*, 1997). *R. lessonae* is not as aquatic as *R. ridibunda* or *R. esculenta*, and is usually terrestrial outside the breeding season (Arnold and Burton, 1978; Günther, 1997b; Necas *et al*, 1997). In Central Europe, it lives in cooler habitats than *R. ridibunda*, in altitudes up to 750m (Necas *et al*, 1997). Young frogs mature rapidly and become sexually mature after one year (Frazer, 1983).

Its range spreads in a wide band over much of Europe, including Italy and Sicily, but not Iberia or the Balkans. It is sympatric with *R. esculenta* across almost its entire range (Günther, 1997b). It southern limit in the east follows a clear line from northeast Italy to the Black Sea coast (Arnold and Burton, 1978; Gasc *et al*, 1997). Its absence from the Balkan peninsula may be due to its inability to compete with the more thermophilous *R. ridibunda*. To the east, its range extends through Poland and Ukraine, reaching slightly further north than *R. ridibunda*, in Russia and the Baltic States. There are a few occurrences in southern Norway and southeast Sweden, to around 60°N (Gislen and Kauri, 1959; Gasc *et al*, 1997).

Several populations have been recorded in southeast England since the middle of the last century, and anecdotal records may go back even further (T. Gent, pers. comm.). Early literature refers to *R. lessonae* as '*R. esculenta* var. *lessonae*' as the taxonomy of the green frogs was not understood at the time. Not all populations can be linked to recorded introductions, and it has been suggested on many occasions that some populations of *R.lessonae* may actually be native (Bell, 1859; Wolley, 1859; Boulenger, 1884; Gadow, 1904; Fitter, 1959; Buckley, 1986; Snell, 1994; Arnold, 1995; Buckley and Snell, 1995). Smith (1949), however, did not consider any British green frog populations to be native, and Wolley (1859) entertained the possibility that there might have been some Roman introductions. As Fitter (1959) pointed out, however, there is no evidence

Figure 2.29: *R. lessonae* (after Necas *et al*, 1997) and its distribution (after Gasc *et al*, 1997).

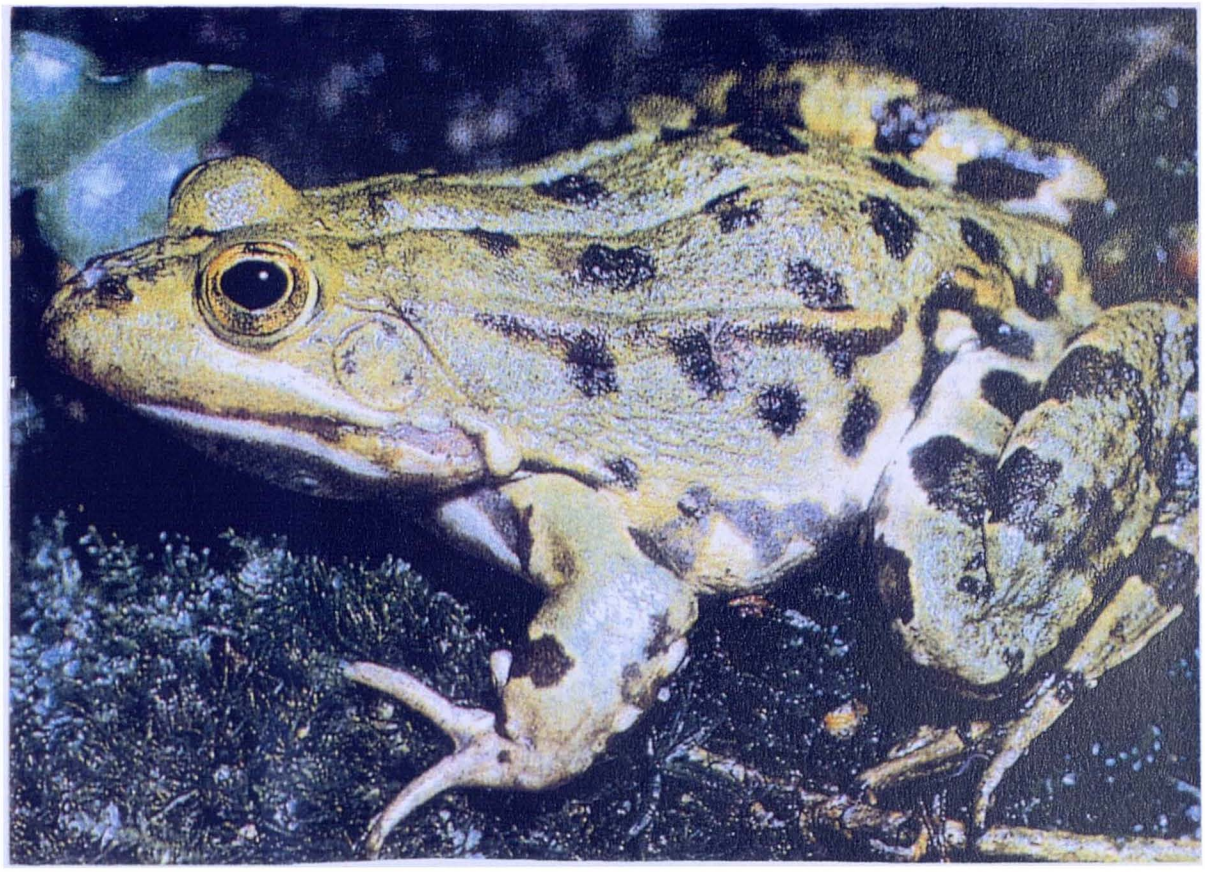
of association with Roman remains. Langton (1996) also disputed suggestions that *R. lessonae* might be native, without any scientific backing for his claim, though Beebee (1996) has since rebutted this claim. The search for proof of native status clearly lies with the discovery of fossil remains.

A colony of *R. lessonae* at Thompson Common in Norfolk may be the last surviving native population (Buckley, 1986). The habitat at Thompson Common is a series of water-filled pingo scars, in various stages of seral succession, and the surrounding area is ancient, open deciduous woodland. A few *R. lessonae* were recorded there in 1995 (Buckley and Snell, 1995; Snell, 1996), but this population may now be extinct (C. Snell, pers comm.). One surviving male is currently in the care of C. Snell. Boulenger even used specimens from Stow Bedon, near Thompson Common, for the colour plate of *R. lessonae* in his *Tailless Batrachians of Europe* (Boulenger, 1897-8). Another (now extinct) colony at Foulmere Fen, Cambridgeshire, lived within a dense *Phragmites* swamp until it was drained in 1847 (Frazer, 1983). In similarly isolated metapopulations of *R. lessonae* in eastern Sweden, Waldén (1955) argued a mid-18th Century human introduction. Conversely, Forselius (1948) believed that natural immigration took place during the Ancylus period between 9,000-7,500 BP, and Forselius (1962) noted that continued uplift of 60-65cm per century probably contributed to isolation of some island populations. In support of this view, Sjögren (1991) calculated that the observed low 'genetic drift' in the eastern Swedish populations could only be accounted for by long-term isolation rather than recent introduction. Thus it seems that natural immigration of *R. lessonae* into northern peripheral areas, whilst land-bridges still persisted, is a plausible theory for the origin of relict populations.

Fossil remains of *R. lessonae* were recorded from Cudmore Grove (Holman *et al*, 1990), and indeterminate green frog remains were found at Shropham (Holman and Clayden, 1992). The validity of these identifications should be viewed with some caution, owing to the difficulty of identifying green frog bones specifically. In the light of debate over the possible native status of *R. lessonae,* English Nature initiated the *Pool frog* (Rana lessonae) *species recovery programme.* As part of this, the current author has studied herpetological assemblages from archaeological sites in the English Fenland, with the aim of searching for fossil evidence of a long-term presence. *R. lessonae* was found to be present at Gosberton in Lincolnshire, during the Middle Saxon period (Gleed-Owen, 1997e). This record is reported in Chapter 6 and discussed in Chapter 8.

Rana esculenta Linnaeus 1758 **Edible frog**

R. esculenta is a hybrid between *R. ridibunda* and *lessonae*, and not a true biological species. It has been given the term 'klepton', and is sometimes referred to as '*R.* kl. *esculenta*'. *R. esculenta* may have diploid or triploid chromosomes, and can therefore interbreed with either parent species, or with each other to produce more *R. esculenta* (Arnold and Burton, 1978). Diploid animals can mate with either of the parent species, to produce further *R. esculenta* or more offspring of the respective parent species. Triploid edible frogs can mate with each other, and produce offspring



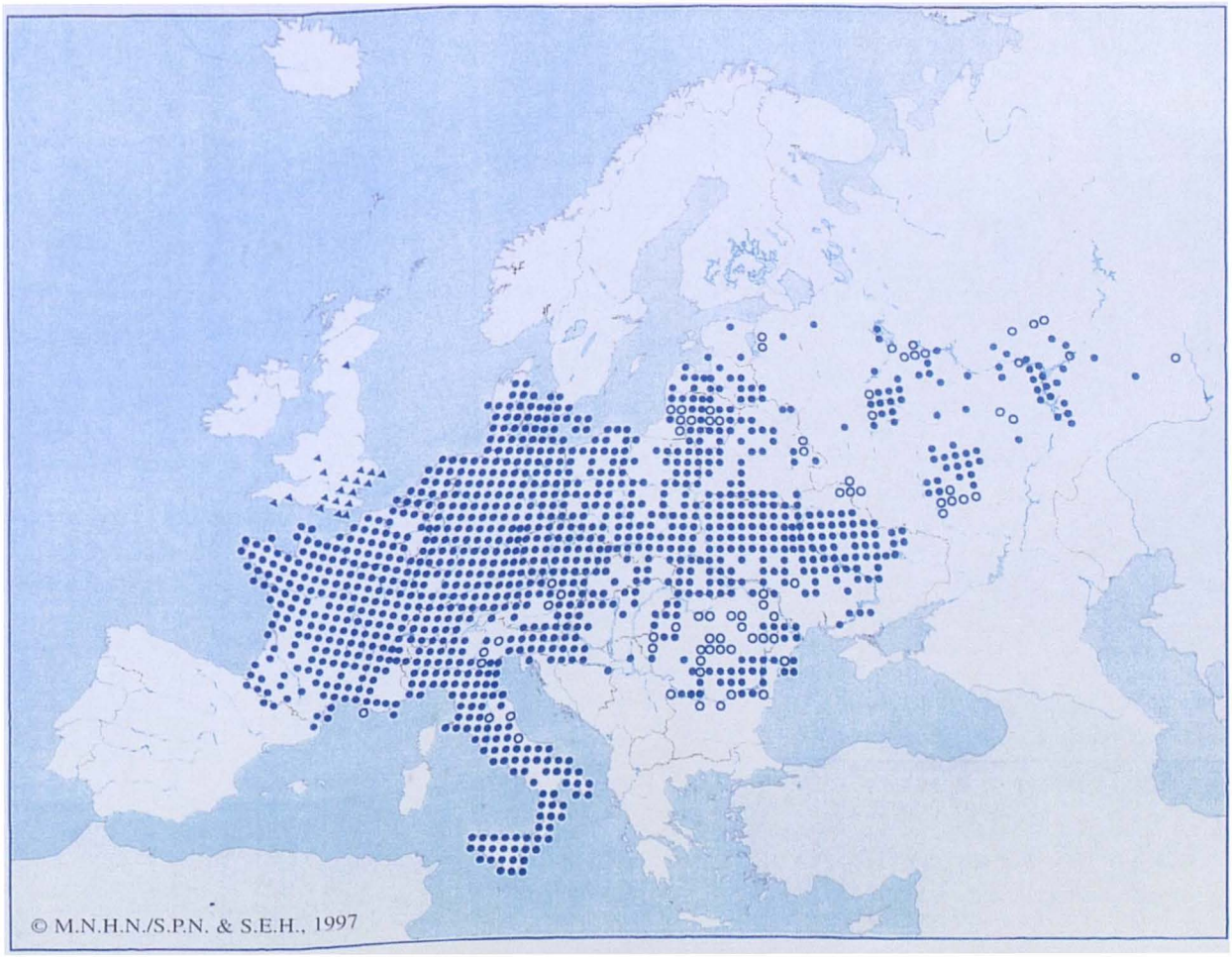


Figure 2.30: *R. esculenta* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

which are again *R. esculenta*, or occasionally they may produce one of the parent species. This gives rise to a number of genetically diverse lineages (Necas *et al*, 1997). The exact mechanisms arising in the different forms, and the complex genetic relationships between them, have only recently been fully understood. Its relationship with *R. lessonae*, and areas of sympatry and allopatry are still unclear (Günther, 1997c).

The Weichselian Lateglacial and Holocene site of Pisede (Germany) produced all three green frog species, showing that the present day genetic relationships were already in existence there during the mid-Holocene (Böhme and Günther, 1979). The very small proportion of *R. ridibunda* remains (1-2% of the green frogs found), were interpreted as the results of occasional *R. esculenta* x *esculenta* crosses (Böhme and Günther, 1979).

As might be expected, *R. esculenta* is intermediate, in many ways, between the parent species *R. ridibunda* and *lessonae*. It reaches around 120mm in length, and its legs are of intermediate length. Its colouration is similar to that of *R. lessonae*, but with more the darker thighs and markings of *R. ridibunda* (Arnold and Burton, 1978). Nevertheless, it is difficult to delimit the physical differences separating the genetically different forms of *R. esculenta* from each other, and from the two parent species (C. Snell, pers. comm., 1997). It appears that *R. esculenta* also inherits the combined ecological preferences of its parents. Ecological studies of colonies in Norfolk found that *R. esculenta* showed no preference for water type, and usually lives with one or other of the parent species (Buckley, 1986). In larger ponds, *R. esculenta* tends to be much more plentiful than *R. lessonae* (Frazer, 1983). Buckley (1986) noted that males become sexually mature after only one year, and females in their second year.

The range of *R. esculenta* is almost identical to that of *R. lessonae*, and some records of this species may have been mitakenly mapped as *R. esculenta* (Günther, 1997c). In Europe, it seems that the distribution of *R. esculenta* is intrinsically linked with that of *R. lessonae*. In southern England, around fifteen colonies are thought to exist today (Arnold, 1995), mainly in East Anglia and the southeast, but also one or two in Devon and Cornwall. Most are linked with proven introductions, but some may still be unaccounted for. It is possible that some may also involve *R. lessonae* (Arnold and Burton, 1978). A doubtful record in Scotland (Arnold, 1995) refers to frogs recorded near Edinburgh during the last century, and provisionally called '*Rana scotica*' (Bell, 1839). Bell acknowledged that it was generally accepted that these were *R. esculenta*, but did not believe this to be the case himself. The figure he gave does appear to be of a green frog, and it is entirely likely that this record came from an introduction. Fitter (1959) detailed many known introductions of *R. esculenta* throughout Britain, including at least one in Lothian. However, he was incorrect in consistently referring to *R. lessonae* as a southern European form of *R. esculenta.*

Fossil remains of '*R. ridibunda/esculenta*' were recorded at West Runton, Cudmore Grove and Itteringham (Holman *et al*, 1988; 1990; Hallock *et al*, 1990), and indeterminate green frog remains were found at Shropham (Holman and Clayden, 1992).

Class: **Reptilia** Linnaeus 1758

Like amphibians, reptiles are poikilotherms and cannot regulate their own body temperature. They depend on insolation from the sun, either direct or indirect (from beneath heated objects), to become active. In northern Europe, reptiles are only active diurnally, in contrast with the amphibians, many of which are crepuscular or nocturnal. Most reptiles lay shelled eggs containing developing embryos (ovoviviparous), but some bear live young (viviparous). The eggs of ovoviviparous species (e.g. *L. agilis*) must be laid in a dry, warm environment for development to be successful. The diet of most reptiles is carnivorous and often includes other reptiles. Reptiles on the whole are more thermophilous than amphibians, with fewer species reaching high latitudes. One terrapin, five lizard and eight snake species are considered here.

Order: Chelonia

Family: Emydidae Gray 1825

Subfamily: Emydinae Gray 1825

The Chelonia are the shelled reptiles: the tortoises, terrapins and turtles. Their skin is tough and scaly, and their body is enclosed within a bony shell, consisting of an upper carapace and a lower plastron. Tortoises are terrestrial and herbivorous, terrapins are semi-aquatic and mainly carnivorous, turtles are aquatic and generally marine. There are about 300 species worldwide, distributed across most continents and oceans (Arnold and Burton, 1978).

The Emydidae includes about eighty species, mainly in warmer areas of the world. There are three European species; all are carnivorous and feed on fish, amphibians, large invertebrates and carrion. They are largely aquatic, but lay their 3-16 eggs on land in soft dry ground (Arnold and Burton, 1978). *Mauremys caspica* and *Mauremys leprosa* (the other European emydids) have southern European distributions (Gasc *et al*, 1997) and are not considered here.

Emys orbicularis (Linnaeus 1758) **European pond terrapin**

The carapace length of adults is usually less than 200mm, but may occasionally reach around 300mm (Arnold and Burton, 1978). It is coloured dark brownish or black, and usually patterned with lighter (often yellow) markings and streaks. The carapace is roughly elliptical in shape, but its outline is variable, and slightly narrower at the front. The plastron has a transverse hinge which allows some vertical movement of the anterior half. Its feet are webbed and have freely movable digits (Street, 1979). *E. orbicularis* is very aquatic and inhabits shallow still or slow-moving water with an abundance of aquatic vegetation and overhanging plants (Arnold and Burton, 1978). It inhabits bogs, swamps, overgrown ponds, streams, backwaters and lakes, tending to avoid clear water, particularly in rocky environments. It prefers muddy or even brackish water, generally surrounded by thick vegetation (Street, 1979). It often basks around the edge of water, on stones or logs, but is otherwise timid and spends most of its time in water (Arnold and Burton, 1978). Eggs are laid in soft ground, and hatchlings measure only 20mm in carapace length. Growth

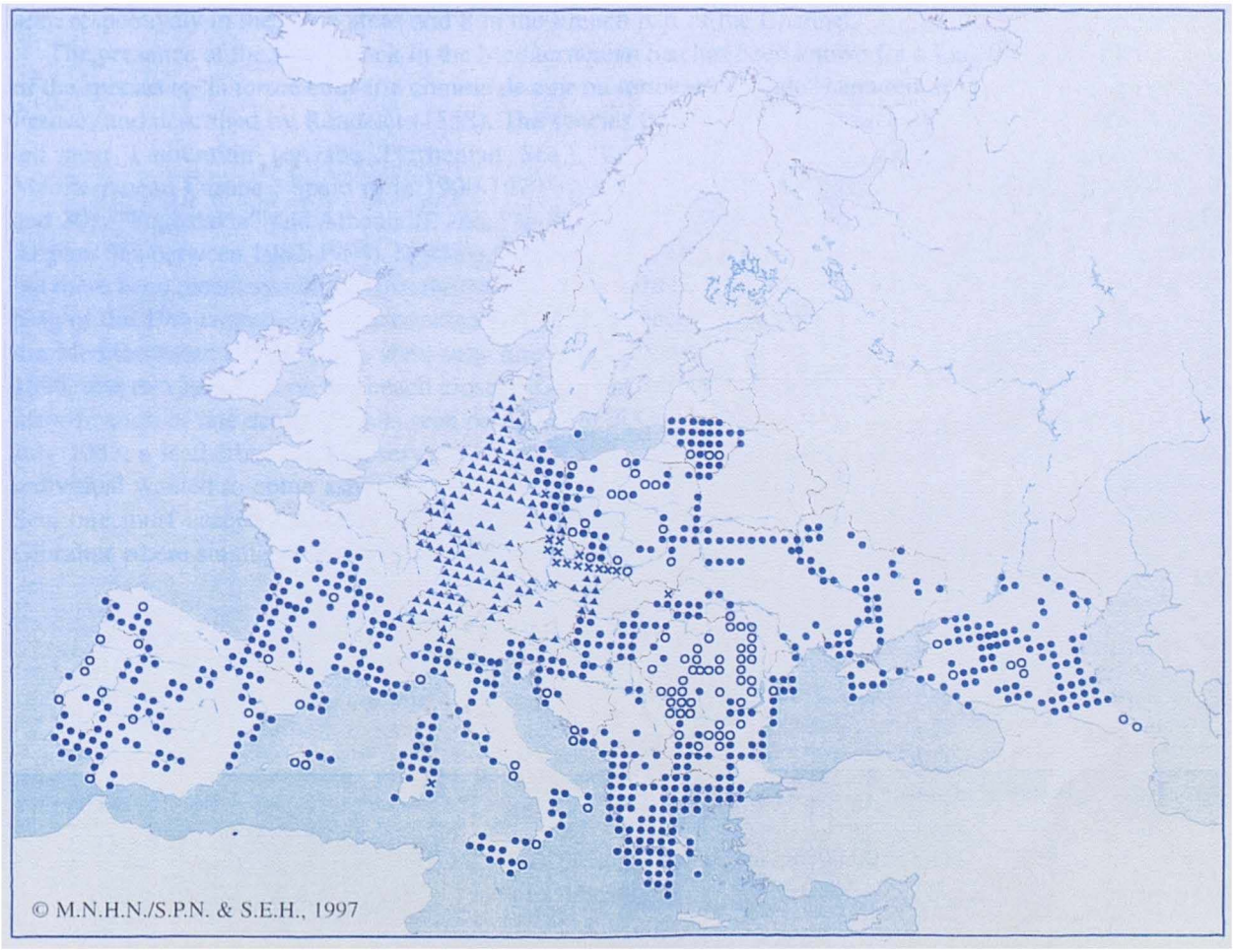


Figure 2.31: *E. orbicularis* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

probably occurs until animals are thirty or forty years old, and longevity can reach 120 years in captivity (Rollinat, 1946).

It is distributed in suitable habitats through most of southern, central and eastern Europe, western Asia and northwest Africa (Arnold and Burton, 1979; Street, 1979). The limits of its European range are rather like that of *R. ridibunda*, but with the addition of Italy. It is absent from parts of central Europe around the Alps, northern France, the low countries and Scandinavia, though it reaches Estonia and Belorussia (Arnold and Burton, 1978; Gasc *et al*, 1997). The breeding success of *E. orbicularis* is clearly linked to summer temperatures, and some northern populations may not breed regularly, especially in years with high cloud cover (Isberg, 1929; Rollinat, 1946; Stuart, 1979). Its northern limit appears to be closely linked with the July isotherm of 20°C, though non-breeding populations almost reach the 18°C isotherm in northern Germany and Poland (Degerbøl and Krog, 1951). It is probable that breeding is occasionally successful in the intervening latitudes, but perhaps only in particularly warm, cloud-free summers.

Introductions to Britain have generally been unsuccessful, though occasional sightings in East Anglia seem to suggest that some long-lived individuals may still persist there (C. Snell, pers. comm.). Many of its recorded occurrences in Denmark, and throughout Germany, are believed to be introductions (Gasc *et al*, 1997). Nevertheless, it appears that in many of these areas, populations were originally present but have become extinct (Podloucky, 1997).

E. orbicularis has been recorded from nine Pleistocene sites in Britain: Westbury-sub-Mendip, Ingress Vale, Cudmore Grove, Stoke Tunnel, Selsey, Swanton Morley, Harkstead, Mundesley and Bobbitshole (Stuart, 1979; Holman, 1987c; 1992d; 1993a; Holman *et al*, 1990; Holman and Clayden, 1992). Fossil remains were also found in Holocene peats, at East Wretham in Norfolk (A. Newton, 1862; Stuart, 1979). Associated pollen spectra suggest a tentative correlation to Holocene pollen subzone VIIa (Hall, 1979). Abundant remains (several hundred individuals) have also been found in Holocene deposits in Denmark, southern Sweden and Germany (Isberg, 1929; Degerbøl and Krog, 1951; Peters, 1977). Comprehensive dating suggests that most lived during the Boreal and Sub-boreal periods when climate was rather continental, with sunny summers, but that some persisted into the early Atlantic (Degerbøl and Krog, 1951). The youngest Danish remains are known from a sacrificial site at Langeland which yielded *E. orbicularis* bones in apparently contemporaneous association with with Iron Age human and domestic animal skeletons dating from c.2,700 BP (Degerbøl and Krog, 1951). The range of *E. orbicularis* therefore appears to have reached its maximum extent during the middle Holocene, and has evidently receded since then, apparently due to worsening summer climate.

Order: Sauria McCartney 1802

Suborder: Lacertilia Owen 1842

The order Sauria consists 2500 species and contains most of the lizards. Along with the snakes, they are included in the Superorder Squamata Oppel 1811.

Family: Lacertidae Bonaparte 1831

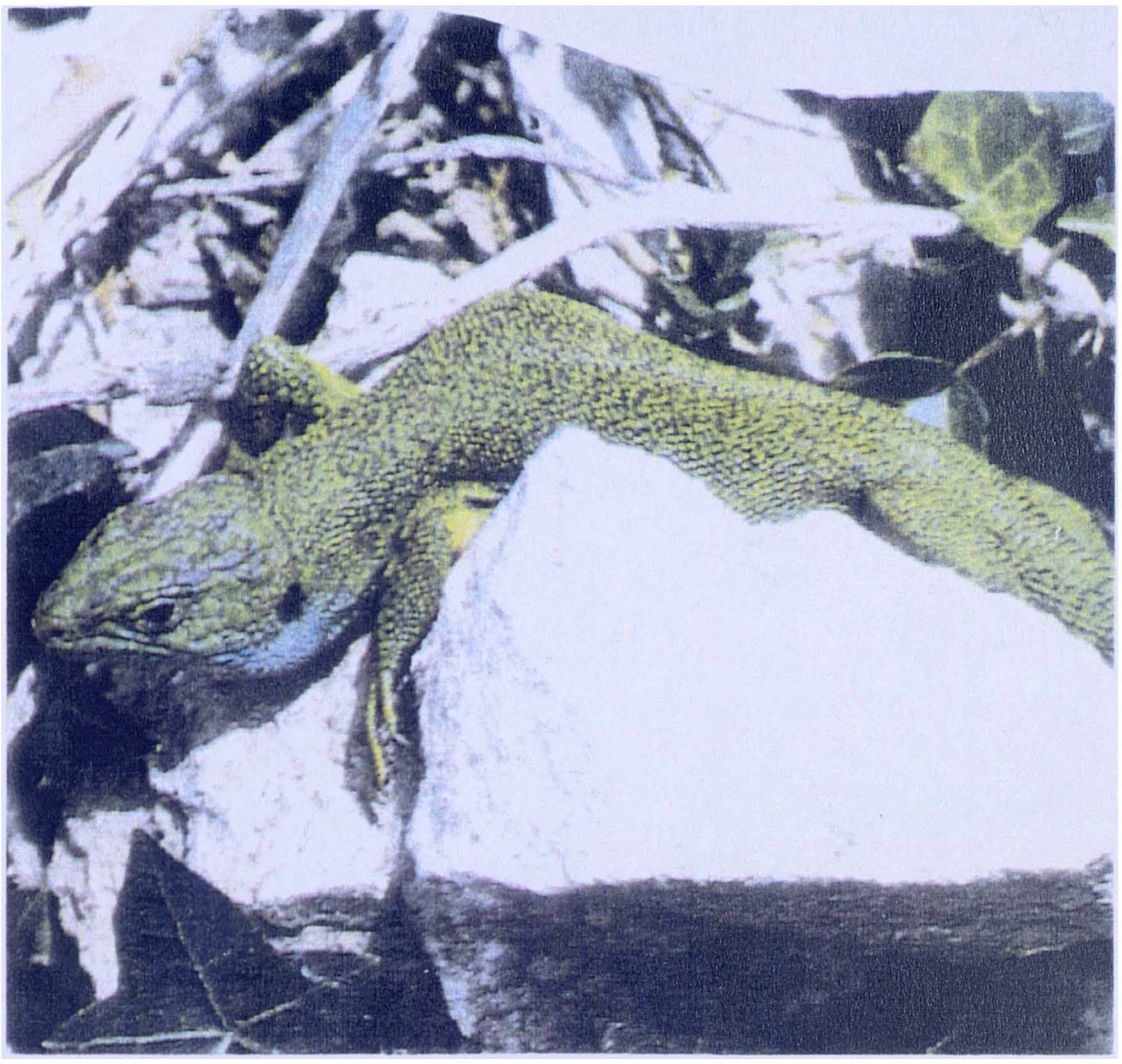
The family Lacertidae is the typical lizards, with most of the European species belonging to it. They have cylindrical bodies, long tails and powerful limbs, the hindlimbs being longer than the forelimbs. Sexual dimorphism is common, with males tending to be brightly coloured, especially so in the breeding season, when they are also territorial and aggressive (Mattison, 1992). All lacertids can deliberately amputate, or autotomise, their own tail when caught by it. The bright colouration, and writhing of the detached tail, helps to keep an attacker occupied whilst the lizard escapes. To facilitate autotomy, all tail vertebrae have a transverse suture acting as a line of weakness, which is broken by muscle contractions during autotomy (Leighton, 1903; Smith, 1969). Regrowth occurs, but only a rod of cartilage replaces the lost vertebrae (Arnold and Burton, 1978). Four species will be considered here, two of which are native to Britain today, and two which are present in adjacent continental areas.

Lacerta viridis (Laurenti 1768) **Green lizard**

This is a relatively large and robust lizard. Adults may reach up to about 130mm from snout to vent, with the tail often being more than twice this length (Arnold and Burton, 1978). Males are usually entirely green, with a black stippling above, but females are more variable. *L. viridis* is found in a variety of well vegetated areas. Typical habitats include open woodland, bramble and other dense undergrowth, shrubby areas and rough grassland (Arnold and Burton, 1978). In southern areas of its range, it is restricted to damper vegetation and uplands, where it occurs up to elevations of 1800m (Arnold and Burton, 1978). In the north, it is usually associated with drier areas and low altitudes (Street, 1979). *L. viridis* feeds on a variety of invertebrates, but also small birds' eggs and fruit, often climbing and hunting in dense thickets. It basks in exposed vegetation, mainly in mornings and evenings, and uses bushes, rodent burrows and crevices for refuge.

L. viridis is distributed across much of southern Europe, except most of Iberia and the Alps. It is present through all but the northeast of France, including the whole west coast, Brittany, Normandy and also in Guernsey (Arnold and Burton, 1978; Gasc *et al*, 1997). In the north, its main range terminates at 49°N, crossing from France to southwest Russia and Ukraine, though a few populations reach about 51°N (Gasc *et al*, 1997). Its northern limit correlates with the 18°C August isotherm (Naulleau, 1997a).

To date, there are no fossil records of this species in Britain. However, *L. viridis* today reaches the Channel coast of Brittany and Normany, and would have been a potential Pleistocene immigrant to Britain. Leighton (1903) noted that after occasional introductions in southern England, it apparently survived well. There are disjunct populations in northern Germany, and uncertain records in Poland (Arnold and Burton, 1978), suggesting its range was once more widespread.



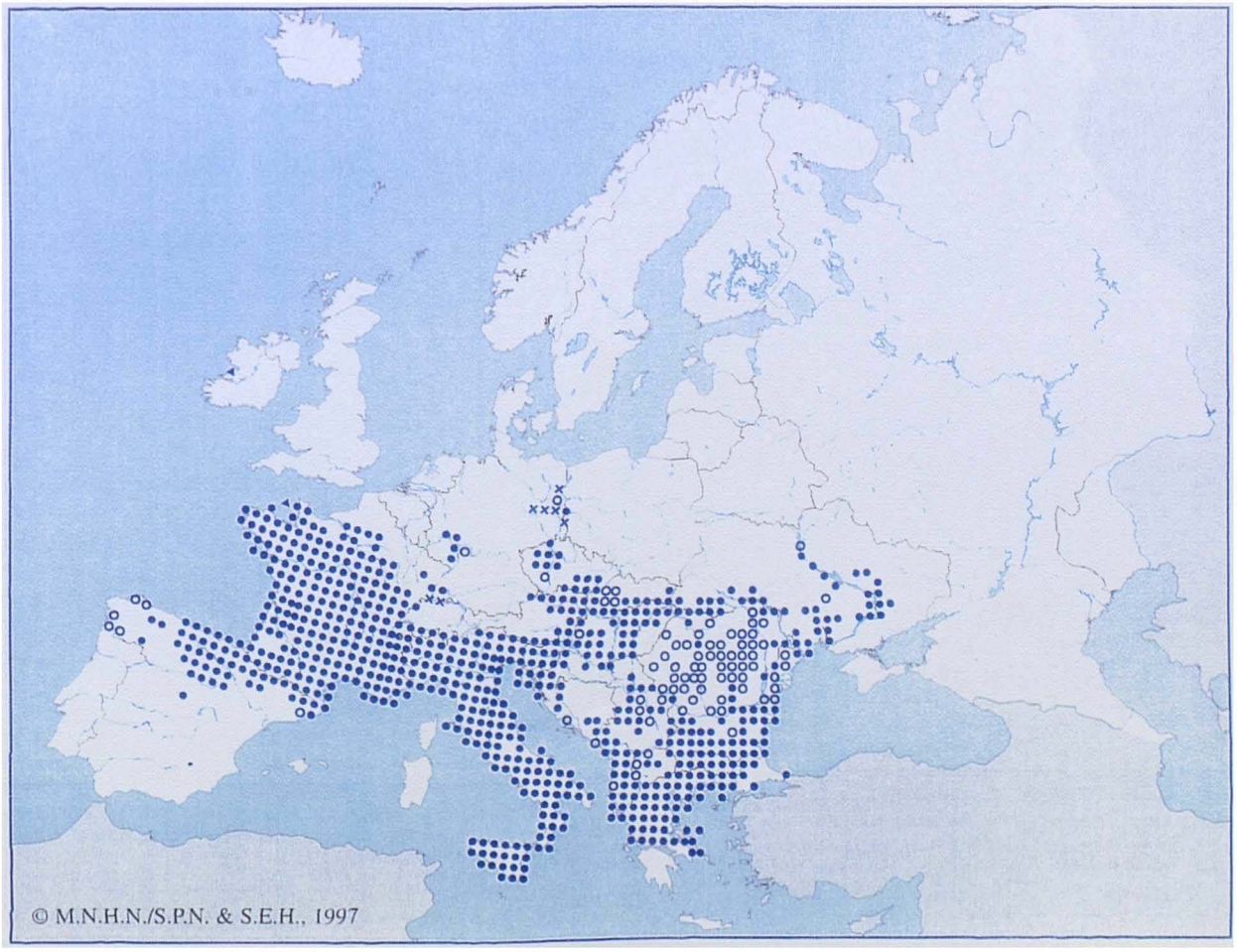


Figure 2.32: *L. viridis* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

Lacerta agilis Linnaeus 1758 **Sand lizard**

Adults can reach about 90mm snout-vent length, though usually smaller, with a tail about one and a half times longer than this (Arnold and Burton, 1978). Sand lizards are short-legged and stocky, with a short deep head, particularly in males. Colouring is extremely variable, though this species is considered a member of the green lizard group. Females are fairly drab, but males generally have green sides, becoming much more brightly coloured during breeding, with a dark symmetrical pattern on the back. This is a lowland species in the north of its range, preferring drier habitats, but in southern regions it has a more upland distribution, reaching up to 2000m (Arnold and Burton, 1978; Korsós and Bischoff, 1997). It is mainly a ground-dwelling lizard, found typically in fairly dry habitats, usually close to dense vegetation. It inhabits a wide variety of such places as grassland, heathland, rough grazing, roadside verges, coastal dune systems, field edges and embankments (Arnold and Burton, 1978; Street, 1979; Korsós and Bischoff, 1997). At the very north of its range, it is restricted to the same dry sandy habitats as *B. calamita*. In the few British locations where it is present, it lives in coastal dunes and in heather on dry sandy heaths.

Its range stretches in a band across central European latitudes, to central Asia. It is restricted to the south, being absent from Iberia, the southern Alps, Italy and the southern Balkans. The northern limit of its distribution crosses Russia, the north Baltic, and a large part of southern Sweden (Arnold and Burton, 1978; Gasc *et al*, 1997). It is present in a few locations in Britain, mainly the Hampshire heaths and the coastal dunes of northwest England where it is found in association with *B. calamita*. It is absent from Ireland and most of Brittany. Its restricted distribution in southern Britain is probably anthropogenic, and the result of heathland losses to farming and afforestation (Beebee, 1978). Its presence in the Sefton Coast requires a much more widespread distribution formerly. In Scandinavia and Russia, it reaches further north than Scotland, and it is present around most of the Channel and North Sea coasts, and throughout the Baltic region. The northern limit of *L. agilis* is apparently restricted by its egg-laying reproductive mode, which is dependant on warm summer temperatures (Mattison, 1992).

L. agilis has not yet been recorded as a British Quaternary fossil.

Small Lacertids

This group of small European lizards contains twenty-four species of the genera *Podarcis* (Wall Lizards) and *Lacerta* (Rock, Meadow and Viviparous Lizards) (Arnold and Burton, 1978).

Lacerta vivipara Jacquin 1787 **Common lizard**

Head and body length can reach around 65mm, but tail length is variable, from about 80-130mm (Arnold and Burton, 1978). *L. vivipara* is a small, but relatively long-bodied lizard, with a small head and thick tail. Its colour is very variable, typically pale brown, though entirely black (melanistic) animals are known. A pattern of irregular, paired white lines and rows of dark brown markings along the back and tail is usual. *L. vivipara* is largely ground-dwelling, but may climb in

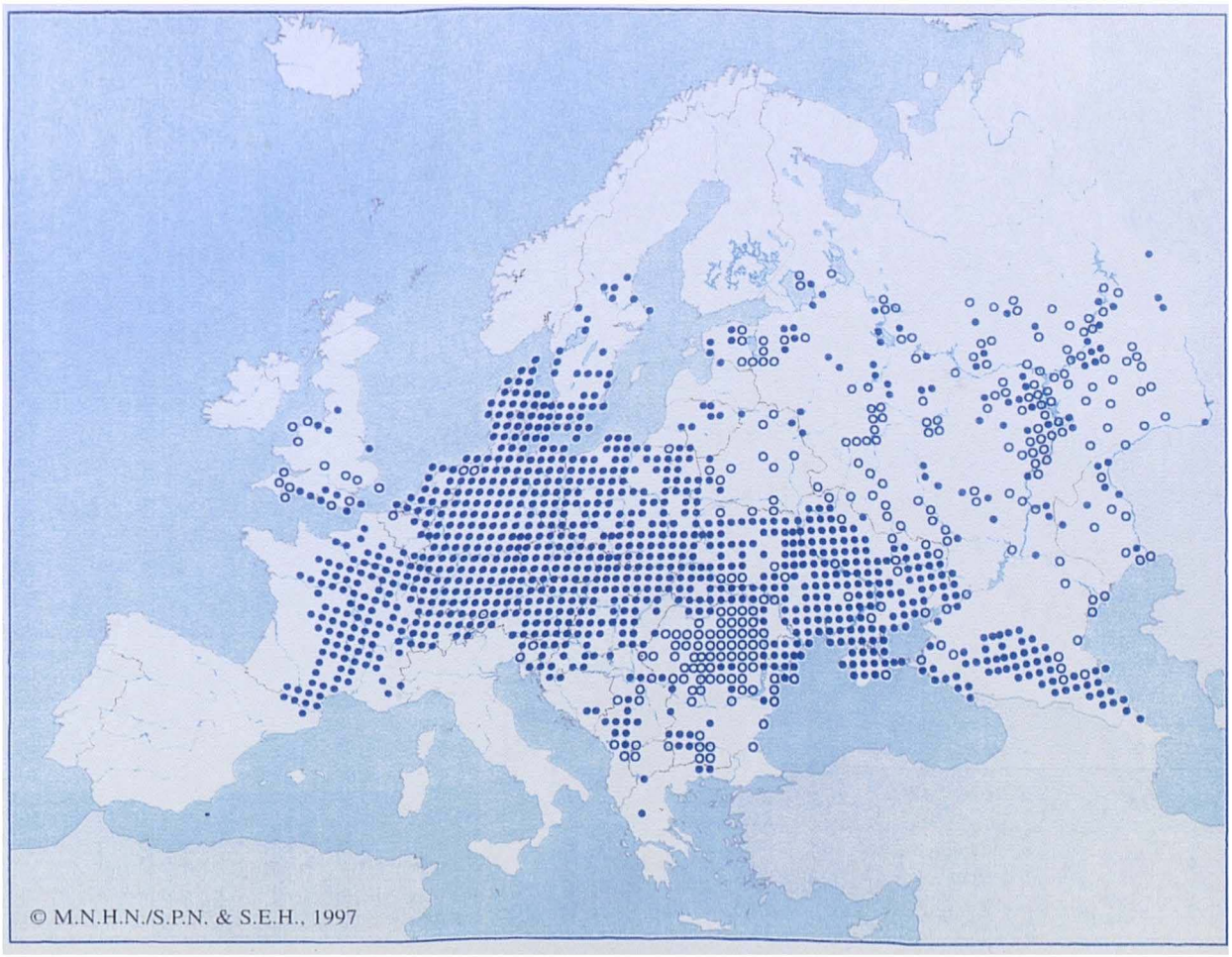


Figure 2.33: *L. agilis* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

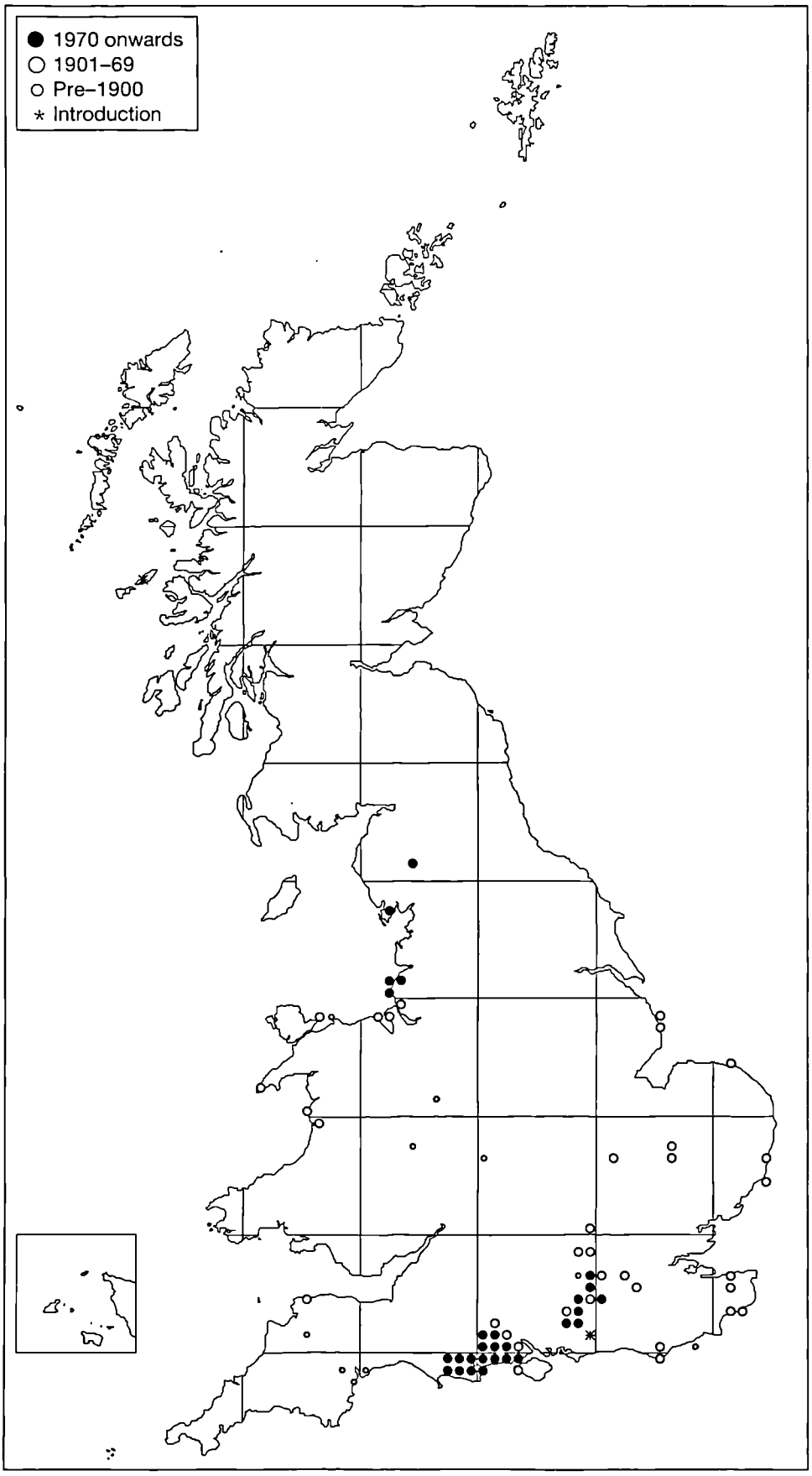


Figure 2.34: Distribution of *L. agilis* in Britain (after Arnold, 1995).

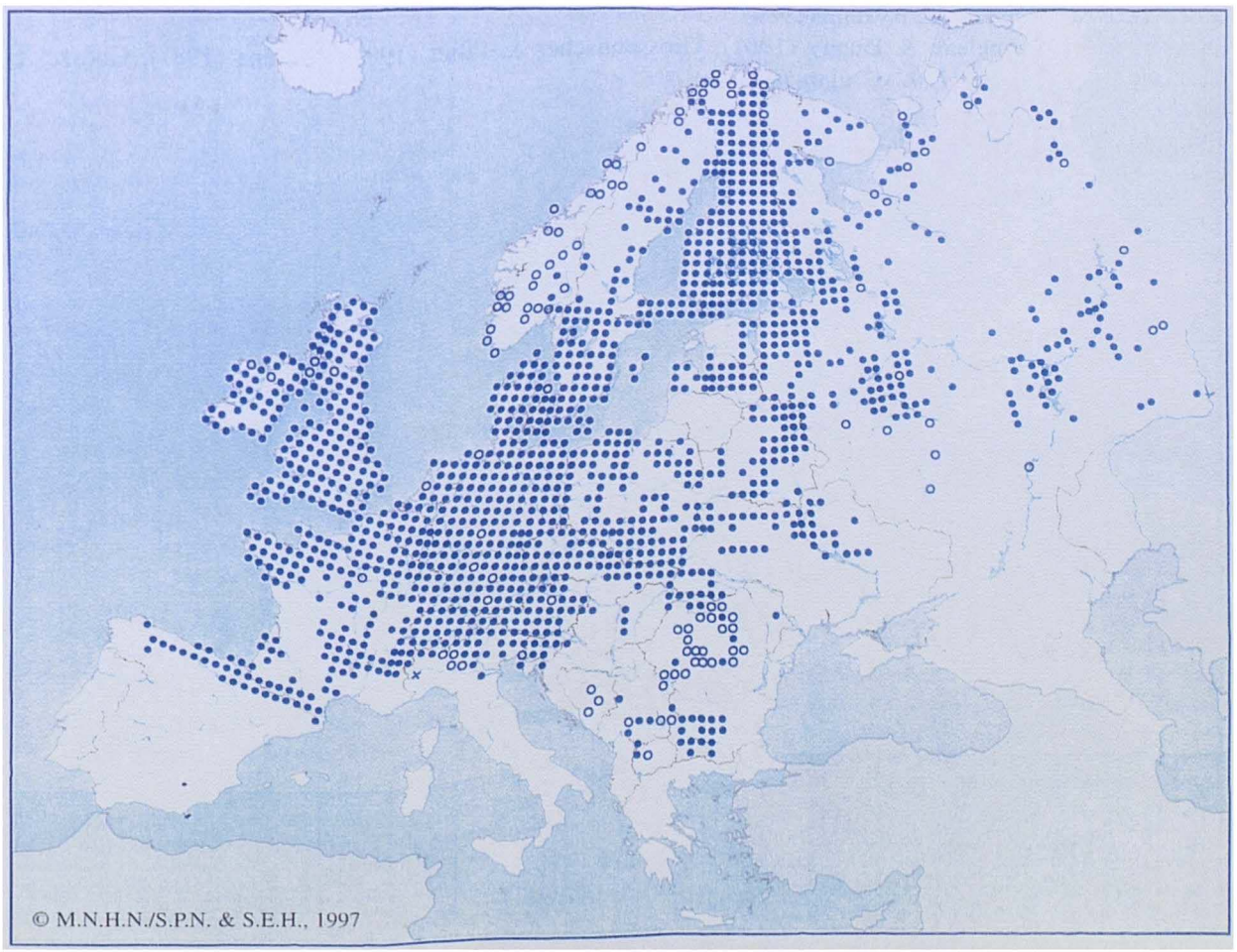


Figure 2.35: *L. vivipara* and its European distribution (after Gasc *et al*, 1997).

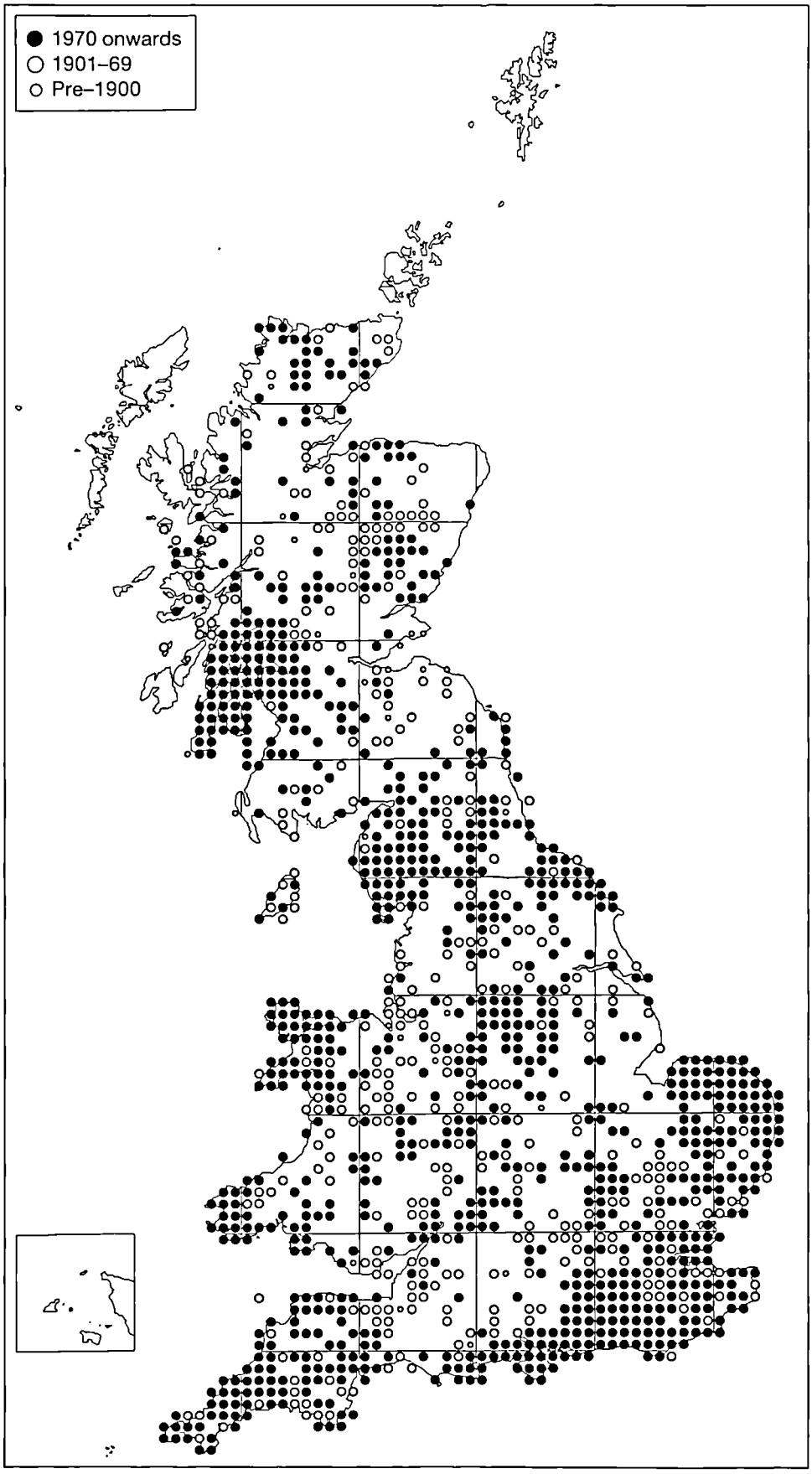


Figure 2.36: Distribution of *L. vivipara* in Britain (after Arnold, 1995).

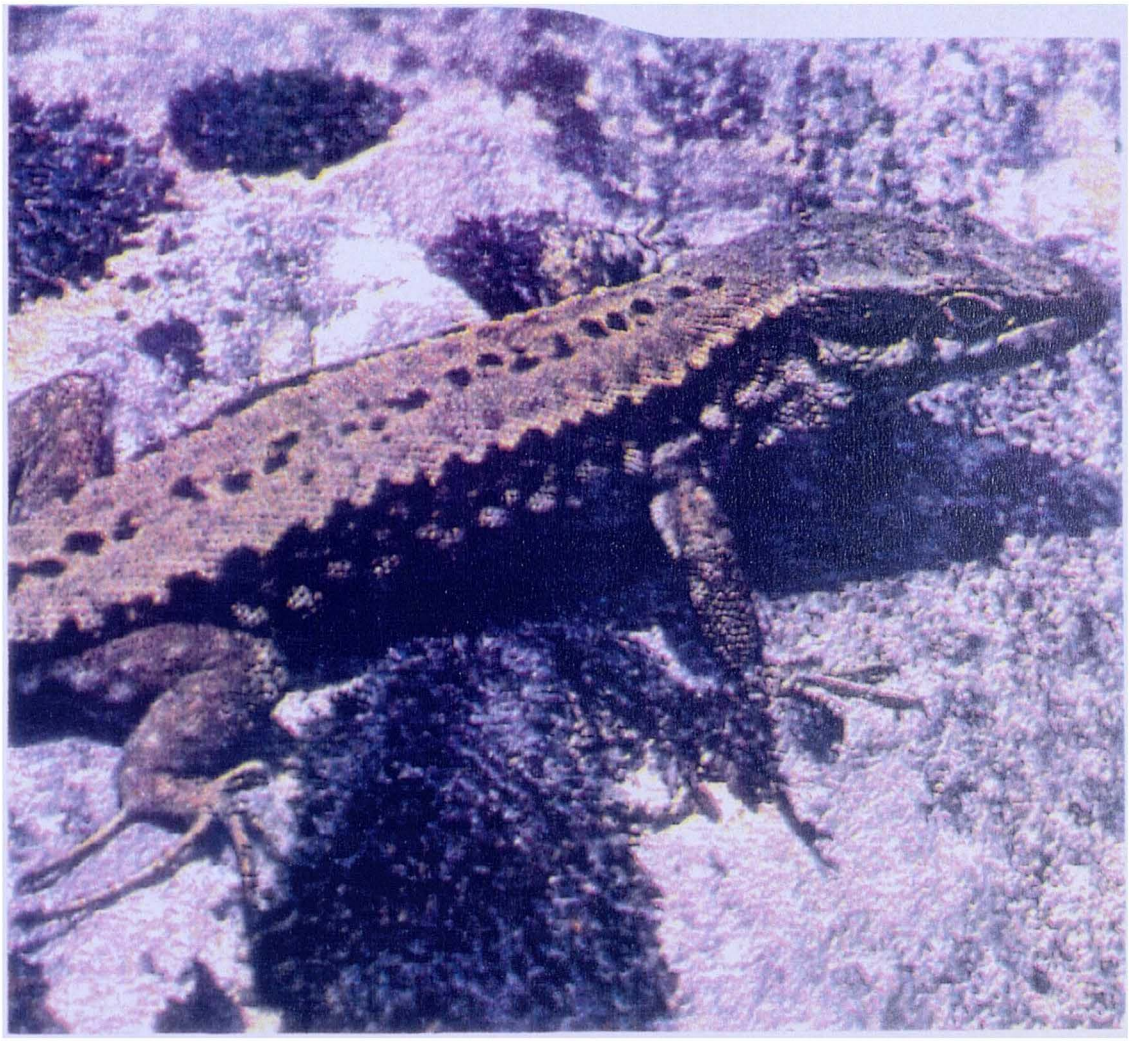
low vegetation. It is considered a typical example of 'Kuehnelt's Principle of Regional Stenoecy', as in the north it is a lowland species, but further south it becomes restricted to progressively higher altitudes (Böhme, 1997). It is found in humid environments, typically in grassland, woodland edges and amongst herbaceous vegetation. In the south of its range, it is confined to moister mountainous areas such as alpine meadows, marshes and damp woodland edges, ascending up to 3000m in the Alps (Arnold and Burton, 1978; Böhme, 1997). In northern regions, it is more widespread and distributed throughout a range of habitats, including grassland, open woodland, coastal cliffs, heaths, moors, bogs and sand dunes (Arnold and Burton, 1978; Street, 1979; Böhme, 1997). As its name implies, *L. vivipara* gives birth to live young over most of its range, though populations in the Pyrenées and Massif Centrale lay eggs (Arnold and Burton, 1978; Böhme, 1997). As its young are incubated internally, it can reproduce in higher latitudes than any other reptile species.

L. vivipara is essentially a northern species. It has a Palaearctic distribution which reaches the Arctic coast of Scandinavia, and it thus hibernates for up to six months of the year (Arnold and Burton, 1978; Mattison, 1992). It reaches 70°N in Norway, and is the world's most northerly reptile (Böhme, 1997). Its vast range stretches from northwest Europe, across northern Asia, to the Pacific coast (Arnold and Burton, 1978; Gasc *et al*, 1997). It extends south through much of southern France, and into the central Balkans. There are isolated populations in northern Iberia, but it is absent from hotter southern regions and does not reach the Mediterranean (Arnold and Burton, 1978; Street, 1979). It is present throughout the British Isles, including Ireland.

Fossil remains referred to 'cf. *L. vivipara*' are known from Cudmore Grove, Nazeing and Shropham (Hinton in Allison *et al*, 1952; Holman *et al*, 1990; Holman, 1992a; Holman and Clayden, 1992). These records probably represent *L. vivipara*, but identification of small lacertid bones is difficult and specific referrals cannot be made with certainty. '*Lacerta* sp.' was recorded from Boxgrove (Holman, 1992a), but recent re-examination has shown this to be a misidentification which should be referred to *A. fragilis* (see Chapter 6).

Podarcis muralis (Laurenti 1768) **Common wall lizard**

P. muralis may reach 75mm in snout-vent length, but most animals are smaller than this. The tail is around twice the snout-vent length (Arnold and Burton, 1978). Lizards in the genus *Podarcis* are wall lizards, and have a rather flattened appearance. Most are brown or grey, sometimes tinged green, and often with clearly demarcated black and white tail bars. Across most of its range, *P. muralis* is widespread in many different localites, though in the north of its range, it is more restricted to sunny, sheltered sites. In southern parts, it is more montane, reaching elevations of 1,700m in Switzerland and 2,500m in Greece (Street, 1979; Guillaume, 1997). *P. muralis* is an active and an opportunistic species, more so than other lacertids (Arnold and Burton, 1978). It is generally found in drier places than *L. vivipara*, but may be encountered in more humid and better-vegetated habitats in the south. It typically climbs rock faces, boulders, ruins and tree trunks. In



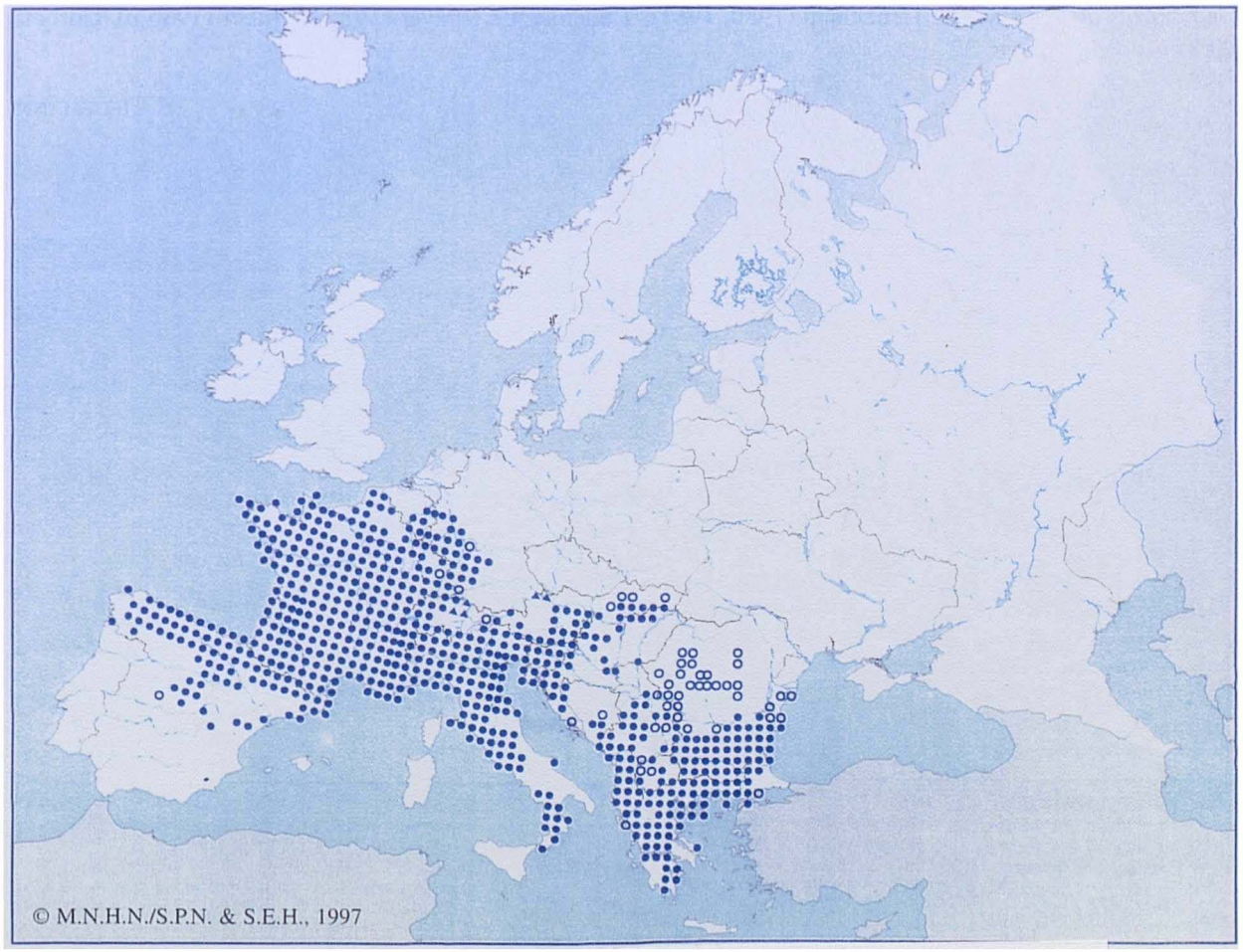


Figure 2.37: *P. muralis* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

the south of its range, it is often found on vegetated screes, grassy banks and sunny woodland glades (Arnold and Burton, 1978). This is a very variable species across its range, mainly in colouration, but also in some aspects of morphology (Arnold and Burton, 1978).

P. muralis is distributed in a band across mainland Europe, with a similar range to *L. viridis, E. longissima, B. variegata* and *R. dalmatina*. In the north, it reaches northeast France, south Belgium and west Germany, with northernmost populations around Maastricht, at 51°N (Gasc *et al*, 1997; Guillaume, 1997). Its southern limit spans most of Italy and the Balkans, except some coastal areas. It is present in northern Iberia and parts of central Spain, and is present in some islands off the Atlantic coast of Spain and France. It is distributed through much of eastern Europe to the Black Sea (Gasc *et al*, 1997), and also extends into parts of Asia Minor (Arnold and Burton, 1978).

Though it is not found in the British Isles, *P. muralis* is present along the French Channel coast and in the Channel Islands, and might be expected as a possible British Pleistocene colonist. It has been successfully introduced at unspecified locations in Great Britain (Guillaume, 1997). At present, no fossil remains are known from British sites.

Family: Anguidae Gray 1825

Subfamily: Anguinae (Gray 1825)

The Anguidae consists 70 to 80 species, of which most are limbless lizards (Arnold and Burton, 1978). Only three species live in Europe, *A. fragilis* the slow-worm, *Anguis cephallonicus* Werner 1894, and *Pseudopus apodus* (Pallas, 1775) the European glass lizard or sheltopusik. The family has a good fossil record, tracing a long ancestry. The earliest known record of the European slow-worm dates back some 25 million years, with little change in its morphology (Estes, 1983). Perhaps the most distinctive feature of its osteology is its complete covering of bony scales or osteoderms, evolved to suit a fossorial existence. Overall, the skeleton of *A. fragilis* has a regressive body form, reflecting its fossorial existence (Smith, 1969). Like the Lacertidae, anguids will readily autotomise their tail if captured.

Anguis fragilis Linnaeus 1758 **Slow-worm**

A. fragilis may reach around 500mm in total body length, though most are considerably smaller than this. An intact tail is normally somewhat longer than the body, but most adults show signs of breakage, with regeneration being a slow process (Arnold and Burton, 1978). Its appearance is very snake-like, with very smooth scales, and a thick neck which is continuous with the head and body. Its colour is generally grey or brown, with a shiny appearance: females have darker sides and a vertebral stripe; males are usually speckled with blue spots; juveniles are gold with a dark vertebral stripe. *A. fragilis* inhabits well-vegetated places, with a dense cover of grass and herbage, and is often associated with fairly damp habitats. It is typically found in meadows, lush grasslnad, woodland glades, moist heathland and scrub (Arnold and Burton, 1978). In Central Europe, it is

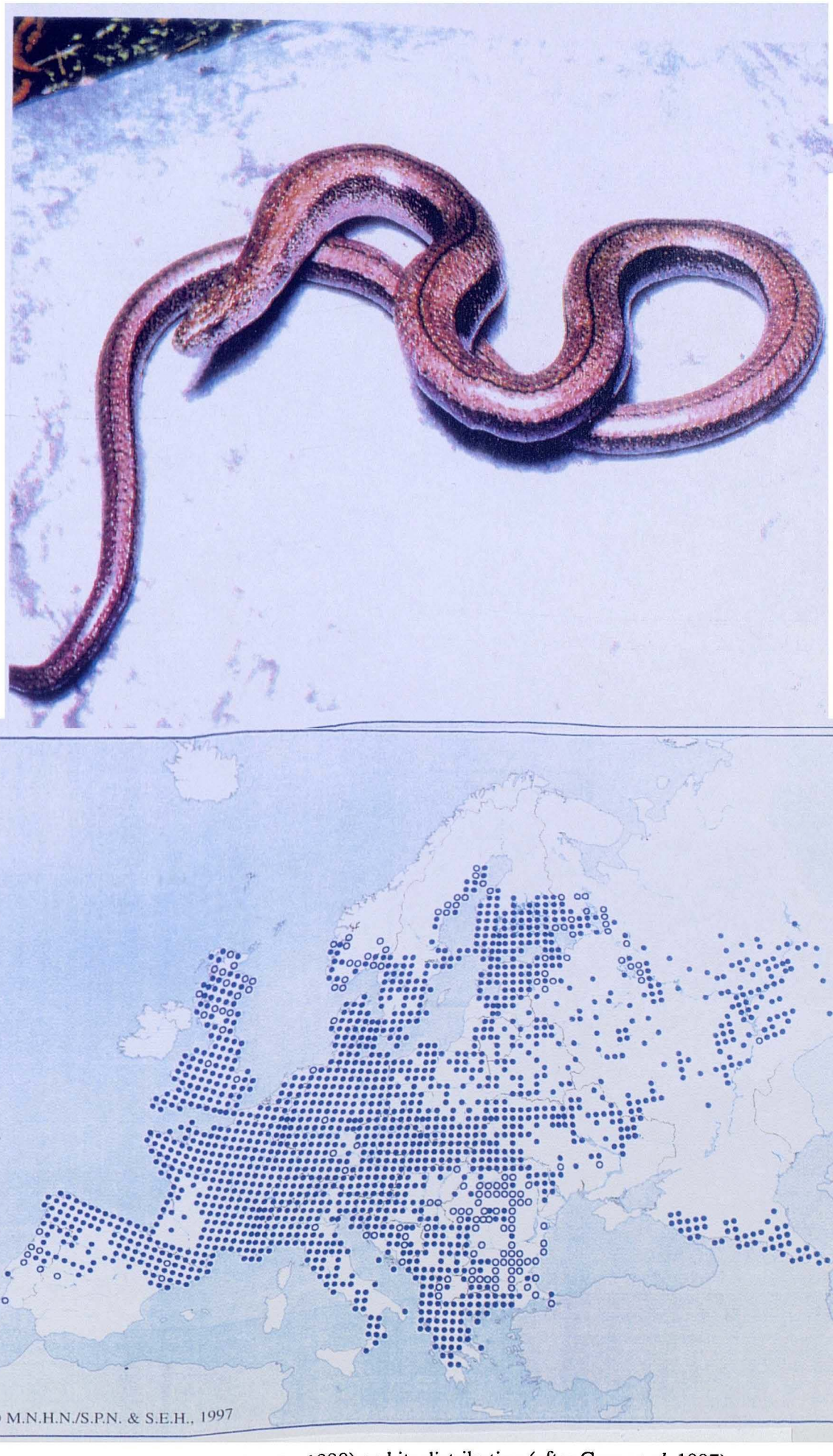


Figure 2.38: *A. fragilis* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

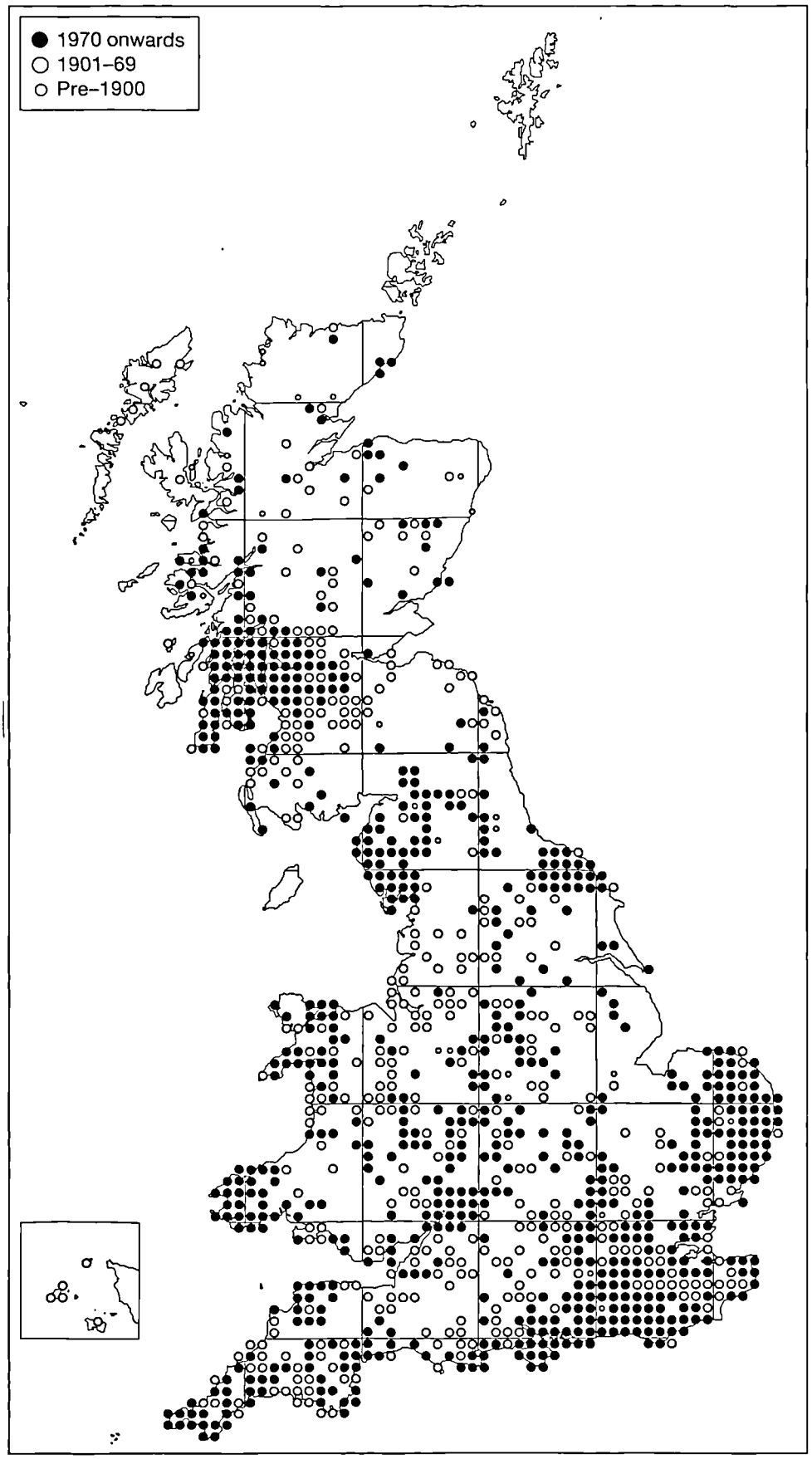


Figure 2.39: Distribution of *A. fragilis* in Britain (after Arnold, 1995).

found in a wider variety of habitats, and was described by Necas *et al* (1997) as 'ecologically adaptive'. It is usually slow-moving and secretive, but it is capable of moving very quickly. It spends most of its time concealed low in vegetation and leaf-litter, and in upper soil layers. Its diet consists largely of slugs and other invertebrates, for which it forages in decaying vegetation (Mattison, 1992).

Its range covers western and Central Europe, but not many Mediterranean areas or Ireland (Gasc *et al,* 1997). It extends eastwards to the Urals, the Caucasus, and some of southwest Asia (Arnold and Burton, 1978). During Pleistocene cold stages, *A. fragilis* is believed to have had disjunct populations in Iberia and Asia Minor, giving rise to different subspecies (Cabela, 1997). Though it reaches northwest Africa, *A. fragilis* is not found in much of southern Iberia, being absent from the dry central plateau. It reaches south to the tip of mainland Italy, the Balkans, and extends as far as 63°N in Finland and Russia, and about 64°N in Sweden (Cabela, 1997; Gasc *et al*, 1997). It is also found in lowland parts of southern Scandinavia, and there are fragmented populations in central parts of Scandinavia (Arnold and Burton, 1978; Gasc *et al*, 1997). *A. fragilis* is distributed throughout Britain and reaches northern Scotland (Arnold, 1995). Its northern limit in Scandinavia and Russia (60-64°N) is governed by winter temperatures preventing successful hibernation, and in the south of its range, it is restricted to mountainous regions where there is higher precipitation (Cabela, 1997).

Remains of *A. fragilis* are known from West Runton, Westbury-sub-Mendip, Boxgrove, Barnham, Cudmore Grove, Purfleet, Ightham, Cow Cave and Dog Holes (Holman, 1985; 1987b; 1988; 1989; 1992a; 1993a; Holman and Clayden, 1988; Holman *et al*, 1988; 1990; Ashton *et al*, 1994). Gleed-Owen (1997f) gave an account of fossil finds of *A. fragilis* in Britain to date.

Order: Ophidia Oppel 1811

Snakes have a covering of scales, most have no vestiges of limbs, and their eyes are lidless. Their jaw and rib articulations are adapted for swallowing large prey. Most species lay eggs, but some are viviparous. Twenty-seven of the 2,700 known species are present in Europe (Arnold and Burton, 1978).

Family: Colubridae Oppel 1811

This is a very large and widely-distributed family, representing the typical snakes, and including most of the European species. It forms part of the superfamily Colubroidea Oppel 1811, and the suborder Alethinophidia Nopsca 1923. Six species are considered here. All are relatively long and slender snakes, when compared with vipers.

Coluber viridiflavus Lacépede 1789 **Western whip snake**

C. viridiflavus can occasionally reach 190cm, with males being larger than females, and has a finely tapering tail (Street, 1979). It is a fast and agile snake which hunts by eye (Arnold and Burton, 1978). It is normally dark green or black in colour, sometimes with bright yellow markings, particularly around the head. *C. viridiflavus* avoids is normally associated with dry, sunny habitats, such as bushy and rocky slopes, scrub, open woodland and sandy heaths (Arnold and Burton, 1978; Street, 1979; Naulleau, 1997b). It is often found in hilly and mountainous country, ascending up to 2,000m in the Alps and Pyrenées (Naulleau, 1997b). Activity is diurnal, with much of its time spent basking on exposed rocks. It is able to climb rocks, bushes and trees, skilfully (Arnold and Burton, 1978; Naulleau, 1997b). Food consists mainly of lizards and rodents, but occasionally amphibians (Arnold and Burton, 1978; Street, 1979).

It is distributed throughout Italy, Corsica and Sardinia, most of France except the north, the Pyrenées, and the Alps of southwest Switzerland (Arnold and Burton, 1978; Street, 1979; Gasc *et al*, 1997). Its northern limit is between 47-48°N in France (Gasc *et al*, 1997), and is probably related to both summer and winter thermal minima. It is very common in Italy, but rarer in the north of its range, and is probably absent from some parts of France within its range (Street, 1979).

There are no British fossil records for this species, but as its range reaches western Brittany, *C. viridiflavus* is considered a potential Pleistocene colonist.

Elaphe longissima (Laurenti 1768) **Aesculapian snake**

Adults can reach 200cm in total length, but are usually less than 140cm (Arnold and Burton, 1978). *E. longissima* is usually a fairly uniform grey-buff to olive-brown colour above, but sometimes with faint darker body stripes. It usually inhabits dry open areas of woodland, scrub, and overgrown ruins. In the north of its range it is confined to more sheltered south-facing localities with well-drained soils. In the Italian Alps, it reaches altitudes of 2,000m (Naulleau, 1997c). It constricts its prey and feeds mainly on small mammals such as mice and voles, as well as birds, nestlings and occasionally lizards (Arnold and Burton, 1978). It is an able climber of steep rock faces and walls, and even vertical tree trunks.

It is patchily distributed throughout most of southern Europe, with the exception of Iberia, and eastwards to Asia Minor (Arnold and Burton, 1978; Gasc *et al*, 1997; Naulleau, 1997c). Its northern limit reaches northern France and southern parts of Germany, Poland and Ukraine. There are several isolated populations in Germany, but some of the northernmost are from introductions (Naulleau, 1997c). However, Degerbøl and Krog (1951) reported that *E. longissima* was recorded in the Vordingborg district in the south of Zealand, Denmark, in 1851 and 1863. Therefore, it is probable that, like *E. orbicularis*, its range was formerly more widespread during much of the middle Holocene. Climatic cooling, of summer temperatures in particular, are almost certainly responsible for its subsequent decline. The positions of isolated relict populations mark the

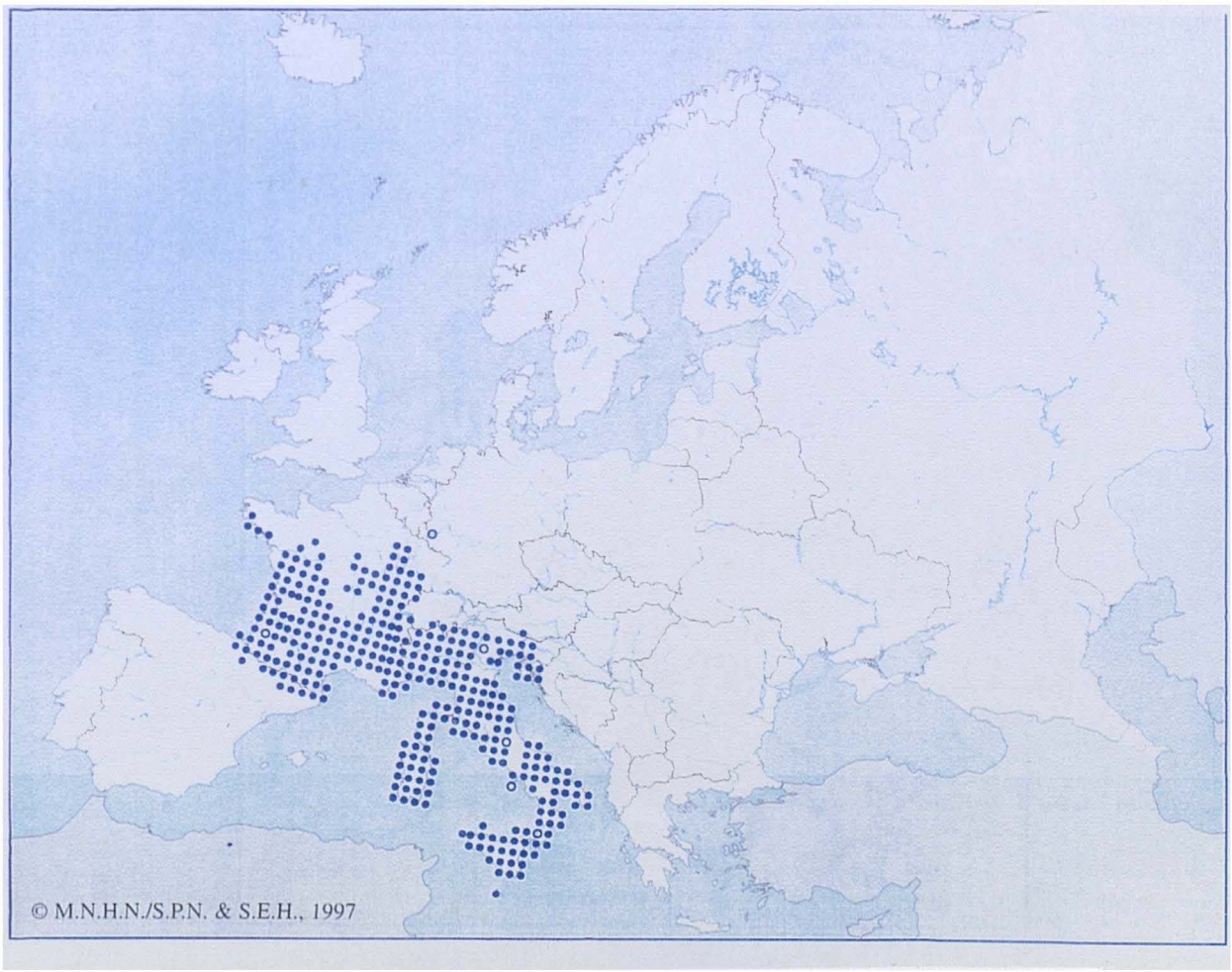


Figure 2.40: *C. viridiflavus* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

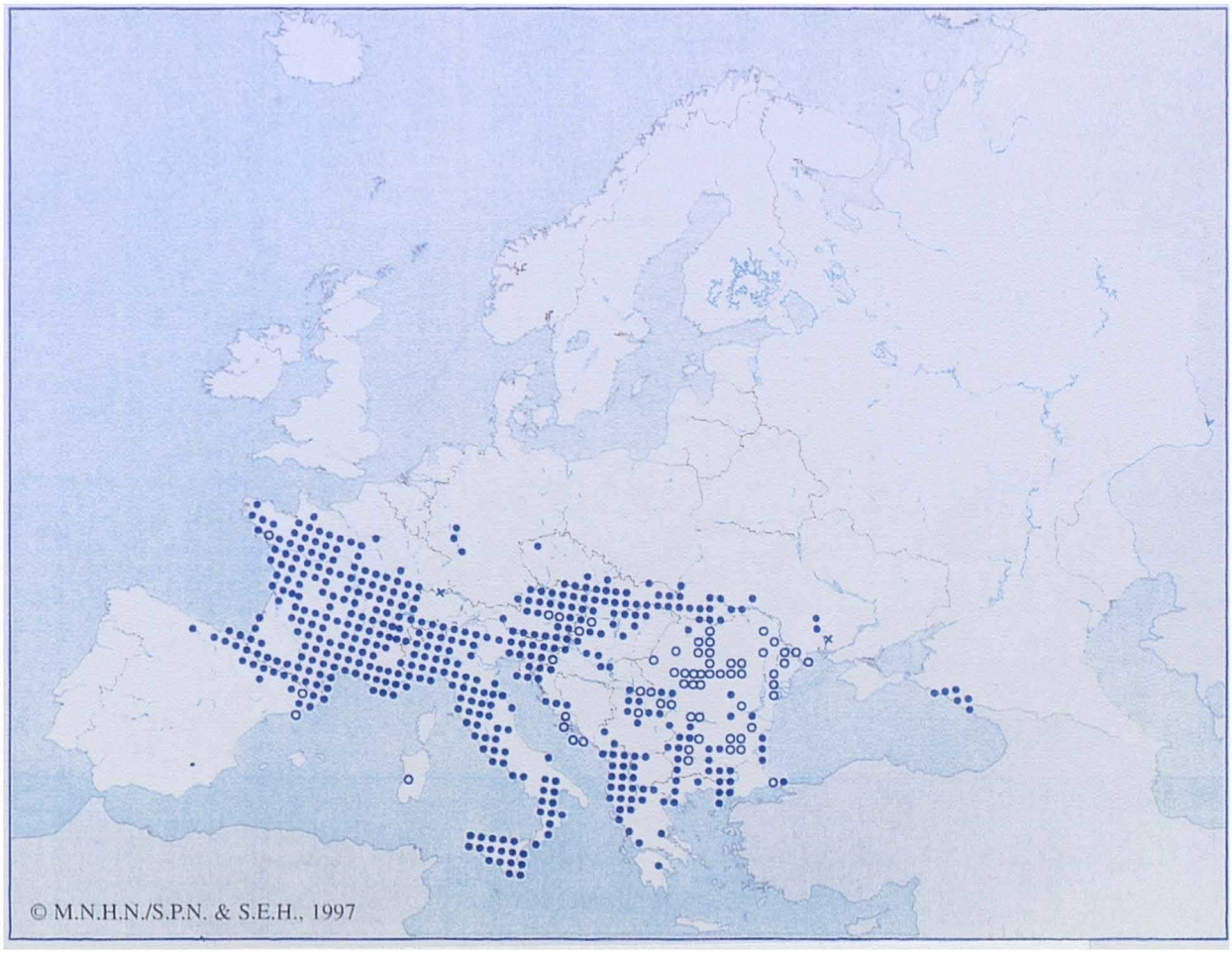


Figure 2.41: *E. longissima* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

minimum extent of what must formerly have been a continuous distribution.

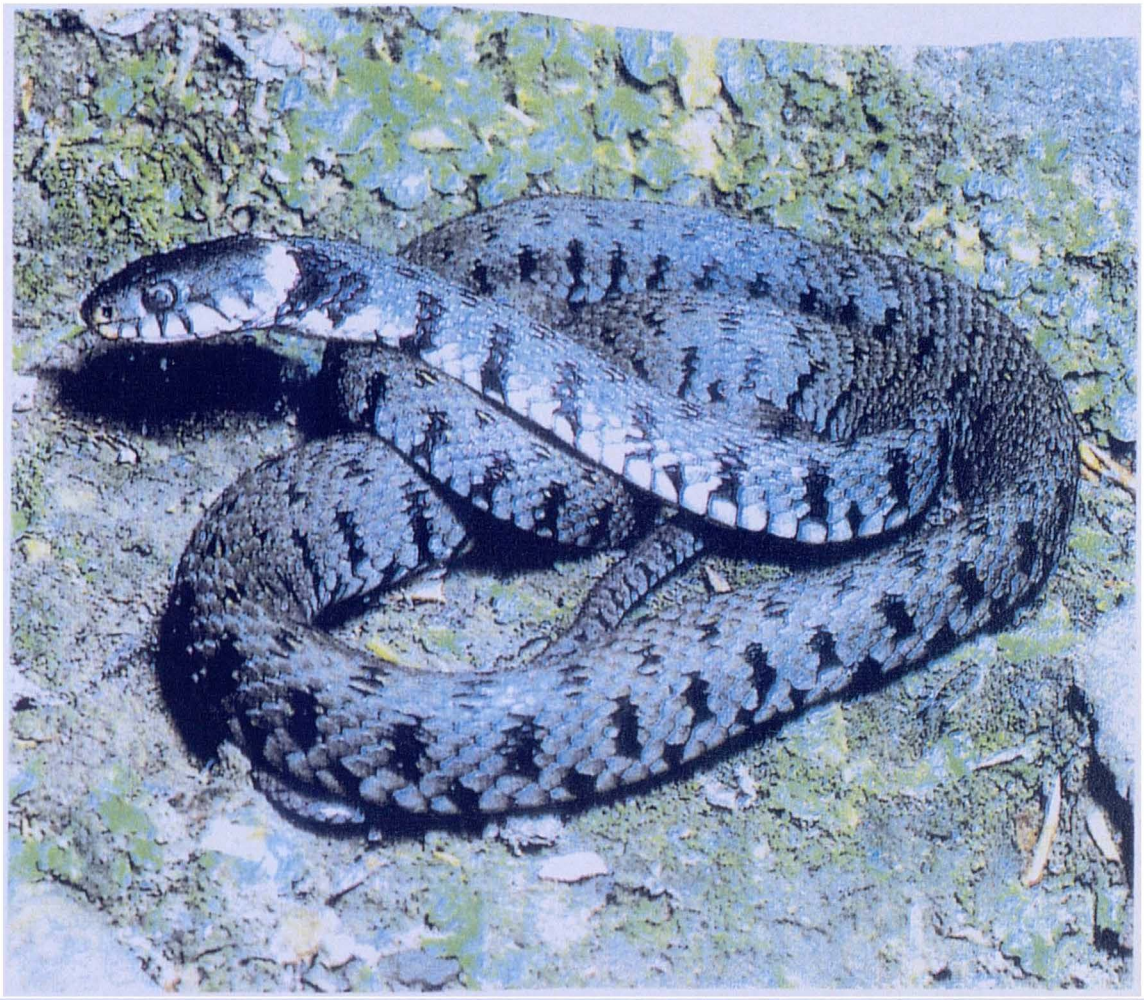
It is not present in the British Isles or northern Europe, but reaches Normandy and Brittany in France. Fossil remains have been recorded from Beeches Pit, Cudmore Grove and Barnham (Holman *et al*, 1990; Ashton *et al*, 1994; Holman, 1994).

Natrix natrix (Linnaeus 1758) **Grass snake**

Most adults are less than 120cm in total length, but females can occasionally reach about 200cm (Arnold and Burton, 1978). Its colour is generally olive-green, with dark bars along its sides, and a distinctive yellow collar behind the head. In most of its range, it is found in damp, well-vegetated places such as meadows, pastures and woodlands. In northern areas it is primarily a lowland species, but lives in a wider range of habitats, sometimes in fairly dry places (Arnold and Burton, 1978). In the south, it may occur up to 2400m, but is more closely associated with damp areas near water. It is less aquatic than *N. tessellata* and *N. maura*, but swims well and often hunts in water for amphibians and small fish (Arnold and Burton, 1978). When attacked, it voids a foul-smelling substance from its anal gland, and may also feign death (thanatosis).

It is widely-distributed and found in almost all of Europe, with a similar range to *A. fragilis* in Scandinavia, where it extends to a latitude of about 67°N (Gislén and Kauri, 1959; Arnold and Burton, 1978; Gasc *et al*, 1997). It reaches northern Sweden around the Gulf of Bothnia, and across southern Finland, Russia, and eastwards to Lake Baikal. Its range extends across southern Europe and into northwest Africa. *N. natrix* is widespread across southern Britain and reaches north to the Scottish borders. There may be some isolated populations in Scotland (Arnold, 1995), but Kabisch (1997) gave south Northumberland as the northern limit in Britain. In Scandinavia, old records extend to 67°N, but in Russia the northern limit is 63°N (Gasc *et al*, 1997). *N. natrix* is oviparous and this is probably the primary control over its northern limits. *L. vivipara, A. fragilis* and *V.berus* reach much further north, but are viviparous, and therefore do not rely on summer warmth to incubate their eggs. Subspecies of *N. natrix* appear to have originated from separate eastern (*N. n. natrix*) and western (*N. n. helvetica*) areas, due to isolation during Pleistocene cold stages (Thorpe, 1979; 1984). Glacial refugia for the western subspecies *N. n. helvetica*, which is now present in Britain, are believed to have been in Iberia and Italy.

N. natrix remains have been found at West Runton, Sugworth, Little Oakley, Westbury-sub-Mendip, Ingress Vale, Cudmore Grove, Barnham, Hoxne, Selsey, Swanton Morley, Shropham, Itteringham, Ightham, Happaway Cave, Dog Holes and Barclodiad y Gawres (Ashton *et al*, 1994; Hallock *et al*, 1990; Holman, 1985; 1987a; 1987b; 1989; 1992b; 1993a; 1993b; Holman and Clayden, 1990; Holman *et al*, 1988; 1990; Lister *et al*, 1990; Newton, 1894; Pumphrey, 1956; Stuart, 1980). Recent re-examination has shown the record from Boxgrove (Holman, 1992a) to be incorrect. The remains appear to belong to *V. berus*, *N. maura* or *N. tessellata* (see Chapter 6).



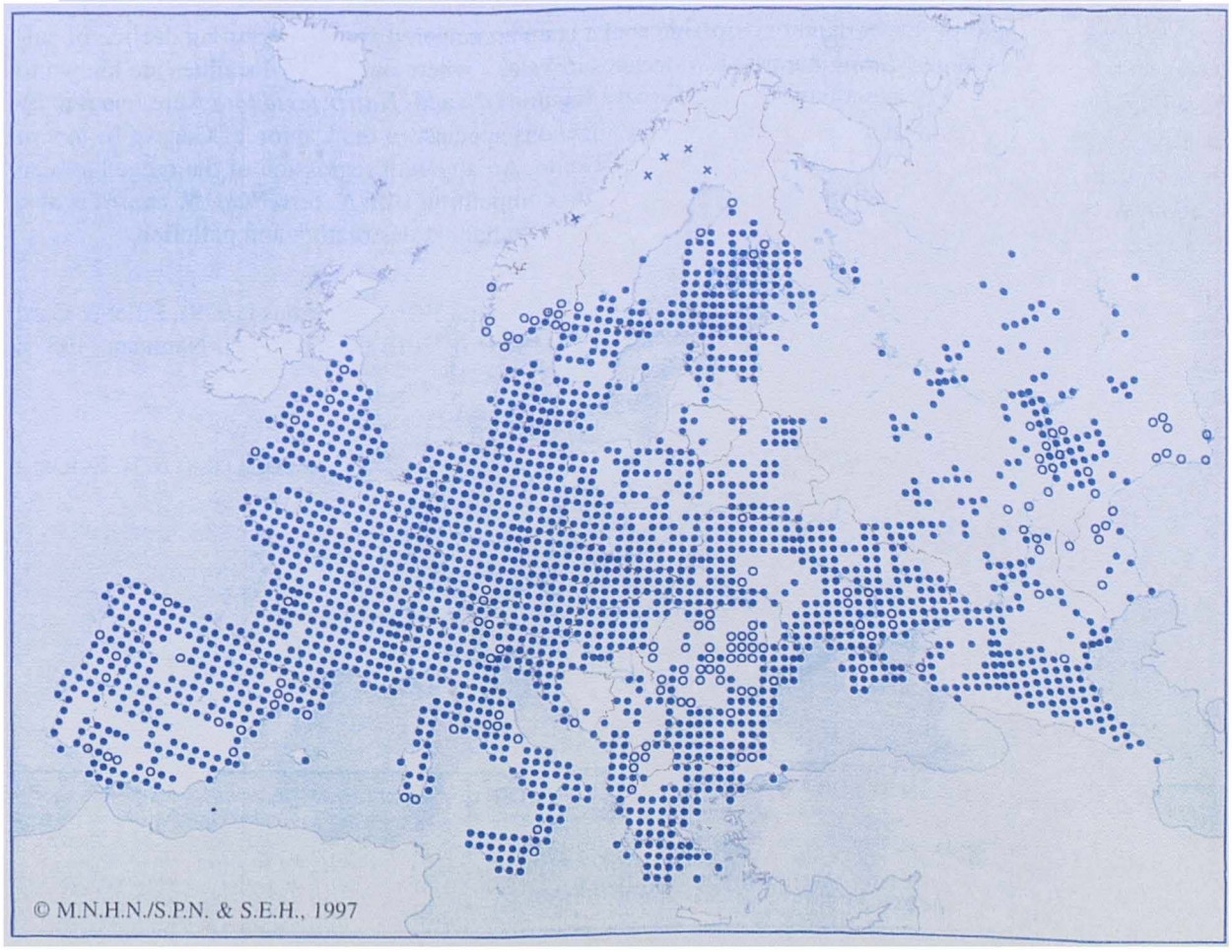


Figure 2.42: *N. natrix* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

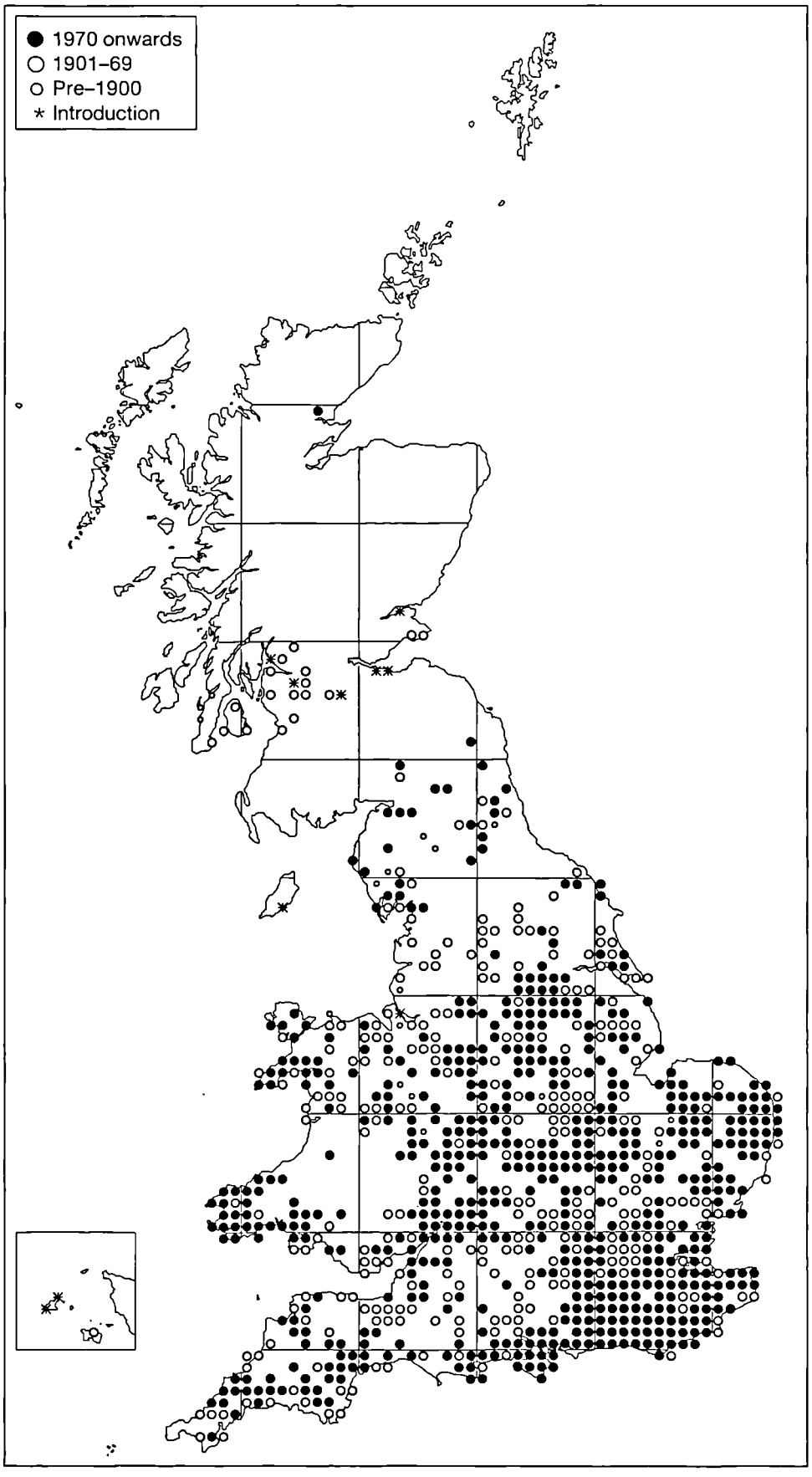


Figure 2.43: Distribution of *N. natrix* in Britain (after Arnold, 1995).

Natrix maura (Linnaeus 1758) **Viperine snake**

This is a relatively small species, usually less than 70cm in total length, but occasionally reaching about 100cm (Arnold and Burton, 1978). Its colour is usually brown or greyish, but may be tinged with red, yellow or olive. There are usually paired rows of dark markings, which may merge into bars or a zig-zag band along the back, giving it a viperine appearance. When threatened, it may flatten its head, hiss, and strike repeatedly, but with its mouth closed; closely imitating a viper (Arnold and Burton, 1978). *N. maura* is a very aquatic species, usually found swimming in water, or resting and basking close to its edge. It prefers weedy ponds, rivers and marshes, but may also hunt in brackish pools and mountain streams (Arnold and Burton, 1978; Street, 1979). It is also found in associated riparian habitats such as damp meadows, grassland and woods. It occurs up to 1400m in the south of its range, but is restricted to lower altitudes in northern parts of its range (Arnold and Burton, 1978; Naulleau and Schätti, 1997). It feeds mainly on amphibians, particularly tadpoles, as well as fish and earthworms (Street, 1979).

N. maura has a western distribution covering Iberia, most of France to 48°N, and reaching northwest Italy. It is also found in the Balearics and Sardinia (Arnold and Burton, 1978; Gasc *et al*, 1997). Its range is largely mutually exclusive with *N. tessellata*, to which it is very similar, biologically and ecologically (Arnold and Burton, 1978).

Bones identified as '*N. maura/tessellata*' were recorded from Cudmore Grove and Shropham (Holman and Clayden, 1990; Holman *et al*, 1990). Specific determination was not possible, but either species could potentially have reached Britain during the Pleistocene.

Natrix tessellata (Laurenti 1768) **Dice snake**

Adults of *N. tessellata* may reach 100cm in total length, but are more usually less than 75cm, with females attaining greater lengths (Arnold and Burton, 1978). Its head is relatively narrow and tapered, and its scales are more strongly keeled than the other European *Natrix*. Colour is variable, but is most often greyish or brownish, though sometimes yellowish or greenish, with a regularly spaced pattern of dark markings in alternate rows. *N. tessellata* has very similar ecological habits to *N. maura*, but is even more aquatic, and spends much of its time in water. It is sometimes found in lowland ponds and lakes, but shows a greater preference to clear, flowing water than *N. maura* (Street, 1979). It is capable of diving for considerable periods, and hunts mainly for fish, though it occasionally feeds on amphibians (Arnold and Burton, 1978; Street, 1979). It is normally found below 1,000m altitude, but in the southeast of its range, it reaches 2,000m or more (Nistri *et al*, 1997).

Its range is essentially southeast European, with some disjunct populations further north. It also extends into southwest and central Asia (Arnold and Burton, 1978; Gasc *et al*, 1997). Its continuous distribution extends north into southern Germany and Poland, and eastwards into southern parts of Ukraine. There are isolated populations around the Rhine and Elbe in central Germany, and in Austria and Switzerland (Arnold and Burton, 1978), indicating that its range was

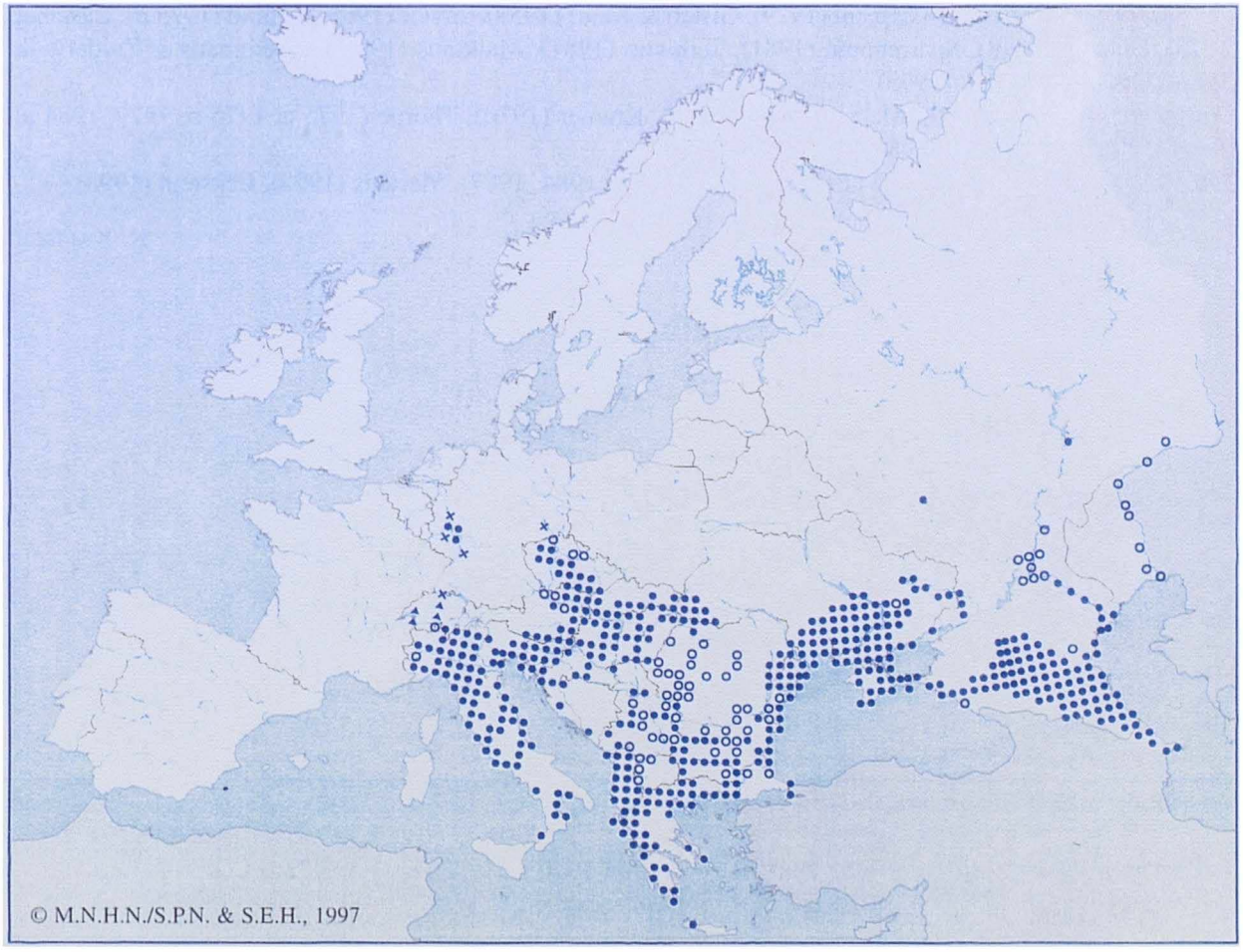


Figure 2.44: *N. maura* (after Coborn, 1994) and its distribution (after Gasc *et al*, 1997).

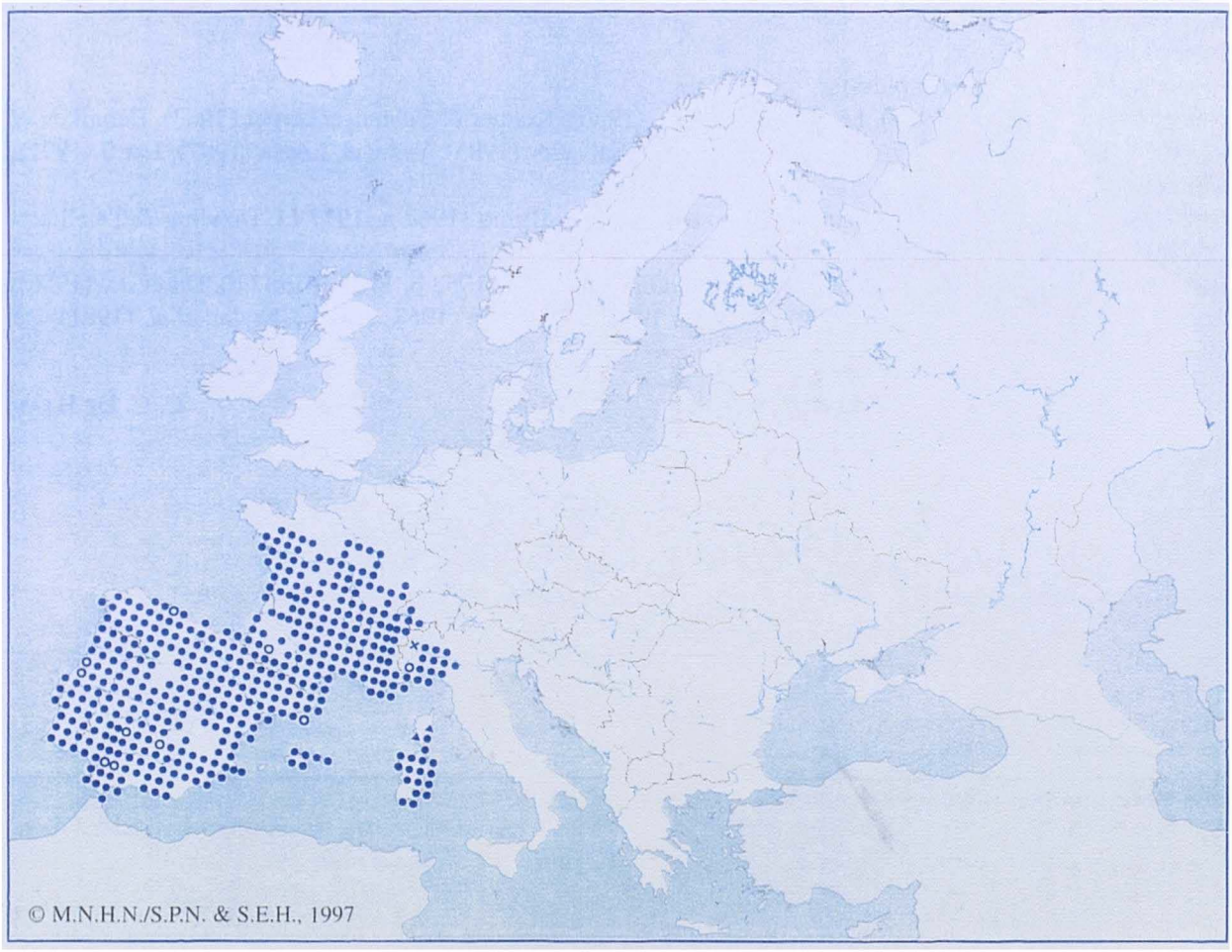
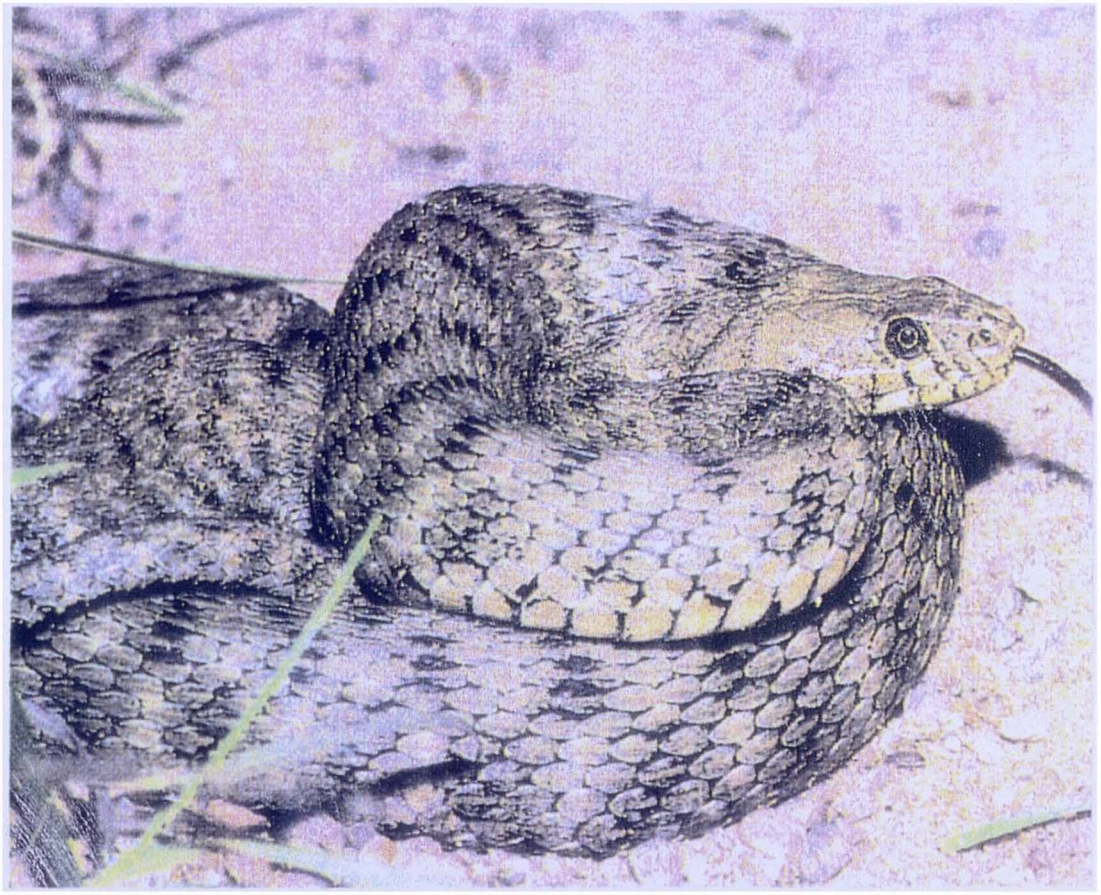


Figure 2.44: *N. maura* (after Coborn, 1994) and its distribution (after Gasc *et al*, 1997).



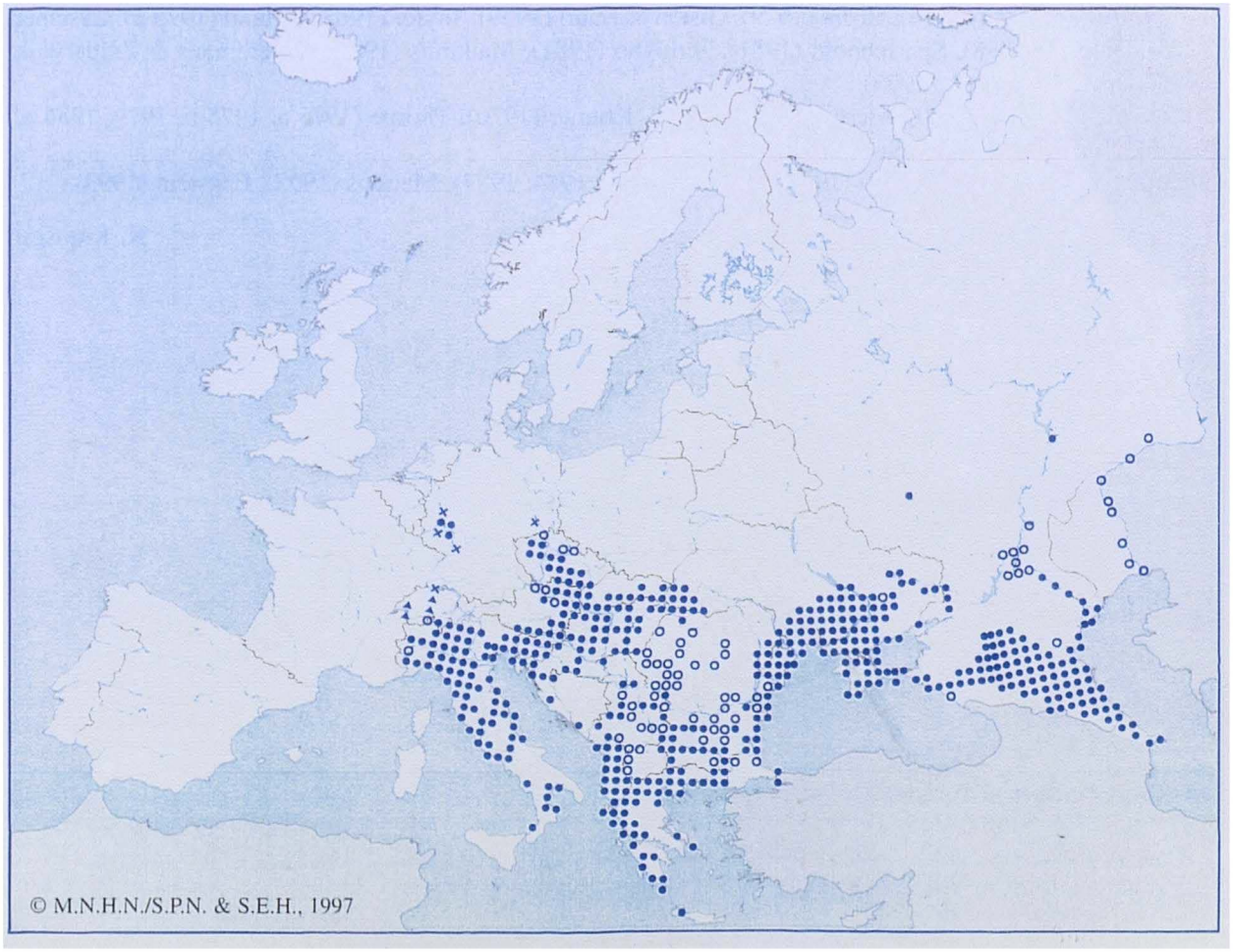


Figure 2.45: *N. tessellata* (after Morrison, 1994) and its distribution (after Gasc *et al*, 1997).

formerly more widespread. Its range is somewhat discontinuous, but no populations reach more than about 48°N (Gasc *et al*, 1997).

Fossil remains, identified as '*N. maura/tessellata*', were recorded from Cudmore Grove and Shropham (Holman and Clayden, 1990; Holman *et al*, 1990), but the authors were unable to differentiate between these two species.

Coronella austriaca Laurenti 1768 **Smooth snake**

C. austriaca is a relatively small snake, generally up to 60cm in total length, but occasionally reaching about 80cm (Arnold and Burton, 1978). Its body is more cylindrical, and with a less well-defined neck, than natricine snakes. Its colour is variable but usually greyish, and typically marked with dark spots or bars above. It is a fairly secretive snake which requires dry, relatively open habitats, where exposure to the sun is possible. Across most of its range, it lives in a variety of habitats, such as scrubland, open woodland, dry grassy banks and heathland. In the south of its range, it is mainly a montane species, reaching over 2,000m elevation (Strijbosch, 1997). There it lives in rock piles, screes, cliffs and other sparsely vegetated areas (Arnold and Burton, 1978; Street, 1979). Towards the north of its range, it becomes more associated with sandy or rocky soils in heathland or open woodland (Street, 1979). In southern Britain, it appears to be closely dependent on mature dry heather, but may also be found in open woodland and woodland edges (Braithwaite *et al*, 1989).

It constricts its larger prey and feeds mainly on small lacertid lizards, but also *A. fragilis*, young snakes, small mammals, and even insects. It is believed to be relatively intelligent for a snake (Arnold and Burton, 1978). It is a fairly slow-moving snake, but will bite an attacker readily, and void a foul-smelling anal secretion. *C. austriaca* is ovo-viviparous, producing between two and fifteen fully formed young encased in a membrane, which mature in around four years (Arnold and Burton, 1978; Street, 1979).

C. austriaca has a widespread and continuous distribution across most of Europe, extending eastwards as far as northern Iran. It is absent from much of Iberia, where it is replaced by *C. girondica* (Arnold and Burton, 1978; Gasc *et al*, 1997). In southern England, *C. austriaca* is restricted to a few heaths and woodlands (Arnold, 1995; Beebee, 1978). A survey between 1984-7 estimated that the last remaining populations (in Hampshire, Dorset and Surrey) totalled perhaps 2,000 in number (Braithwaite *et al*, 1989). In Scandinavia, it is found throughout much of southern Sweden and Norway, reaching 60°N, though old records reach over 62°N (Strijbosch, 1997). Strijbosch (1997) reported that *C. austriaca* reached Scandinavia by 10,000 BP, and Britain by 9,500 BP. Holman's (1985) estimated age for the Ightham assemblage was probably the source of the British fossil record. There are further isolated populations in some of the larger Baltic islands, southern Finland and possibly in northern Sweden (Arnold and Burton, 1978). Its northern limit in Scandinavia and the Baltics extends much further north than it does in Britain, obviously governed by warmer, drier summers. It is notably absent from much of Denmark, and

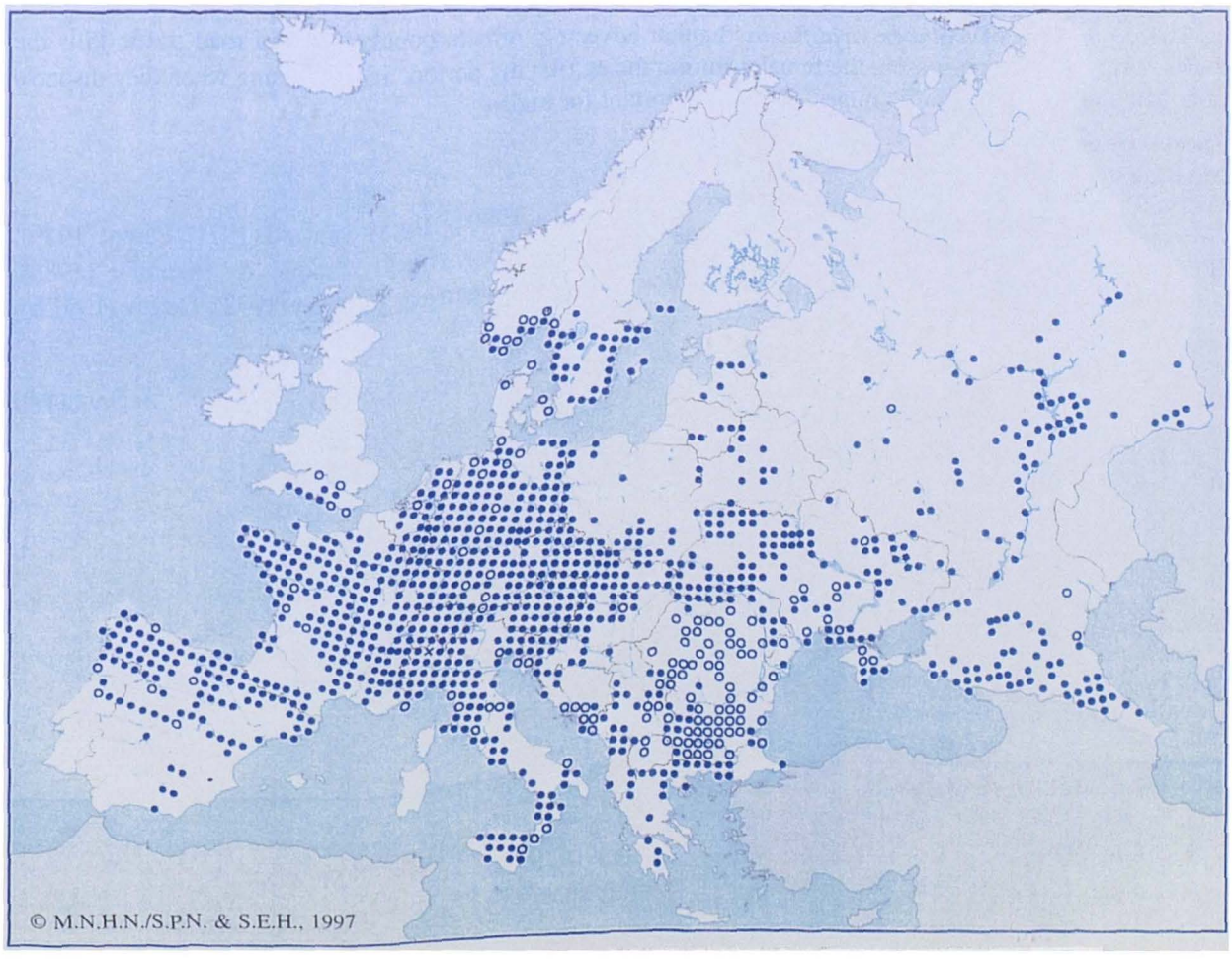


Figure 2.46: *C. austriaca* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

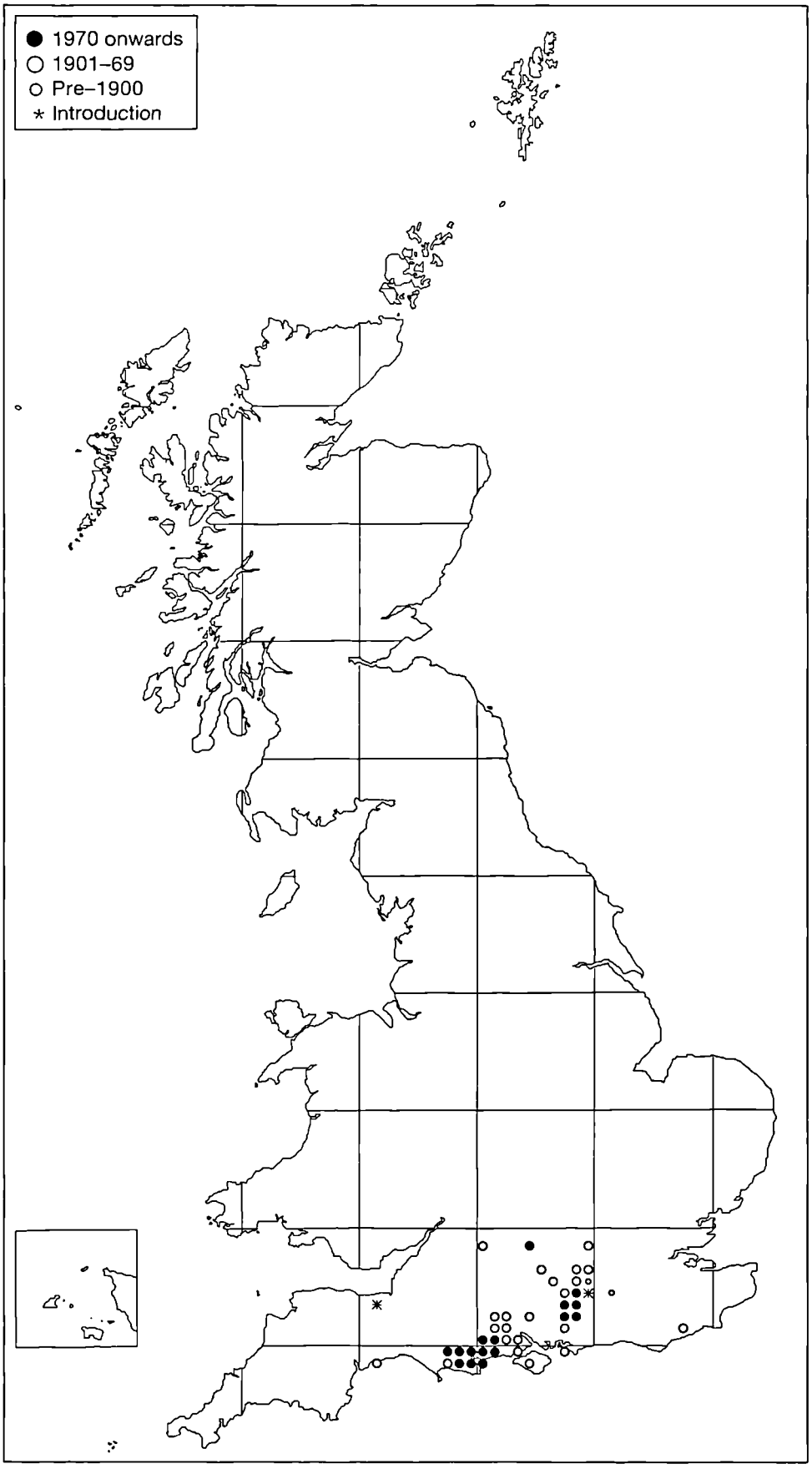


Figure 2.47: Distribution of *C. austriaca* in Britain (after Arnold, 1995).

its range appears to have declined from a formerly wider extent.

Fossil remains of *C. austriaca* have been found at Westbury Cave and Ightham fissure (Holman, 1985; 1993a).

Family: Viperidae Oppel 1811

Subfamily: Viperinae Oppel 1811

The vipers are venomous, relatively short and stout-bodied snakes, of which there are seven European species. Their recent ranges are mainly mutually exclusive, particularly in southern Europe, suggesting that their ecological requirements are similar enough to cause competition.

Vipera berus (Linnaeus 1758) **Adder**

V. berus may occasionally reach 90cm in length, but usually only 60cm or so, and females tend to be longer than males (Arnold and Burton, 1978). It is a thick-bodied snake, with a triangular head, and flattened snout. The body colour is usually reddish brown in females, and blue-grey in males, with a characteristic dark, zig-zag or diamond-patterned vertebral stripe (Arnold and Burton, 1978). *V. berus* occurs in a wide range of habitats, especially in the north of its range. It lives typically in moors, heaths, woodland edges and clearings, marshy meadows, rocky slopes and screes, but avoids clayey soils. It may ascend upland slopes, and in the south of its range, where it is largely montane, it reaches altitudes of 2,600m (Nilson and Andrén, 1997), and possibly 3,000m (Street, 1979). In lowland areas of central Europe and in the south of its range, it is rather sporadic, and is restricted to moister habitats (Arnold and Burton, 1978). *V. berus* feeds mainly on small mammals and lizards, though occasionally on amphibians, and drinks comparatively frequently (Street, 1979). When threatened, it will defend itself by rearing and striking, readily biting its attacker and injecting a potent venom (Arnold and Burton, 1978).

V. berus has a Palaearctic distribution, similar to that of *L. vivipara* and *R. temporaria*. Its northern limit extends beyond the Arctic circle in northern Norway, Sweden and Finland (Arnold and Burton, 1978; Gasc *et al*, 1997), reaching 70°N (Nilson and Andrén, 1997). It is also absent from much of France and Mediterranean Europe, with a disjunct distribution in northern Iberia. *V. berus* is present throughout mainland Britain and some Scottish islands, and reaches the north of Scotland (Arnold, 1995).*V. berus* and *L. vivipara* are the only European reptiles which reach above the Arctic Circle.

Fossil remains of *V. berus* have been identified from West Runton, Westbury-sub-Mendip, Cudmore Grove, Ightham and Cow Cave (Holman, 1985; 1988; 1989; 1993a; Holman *et al*, 1988; 1990; Newton, 1882a; 1882b; 1894).

Vipera aspis (Linnaeus 1758) **Asp viper**

V. aspis can reach a length of 75cm, though usually less, with males tending to grow larger than females (Arnold and Burton, 1978). It has a relatively slender body, with an upturned, snout. It is usually lightly coloured, with a series of dark transverse bars, connected by a thin vertebral streak.

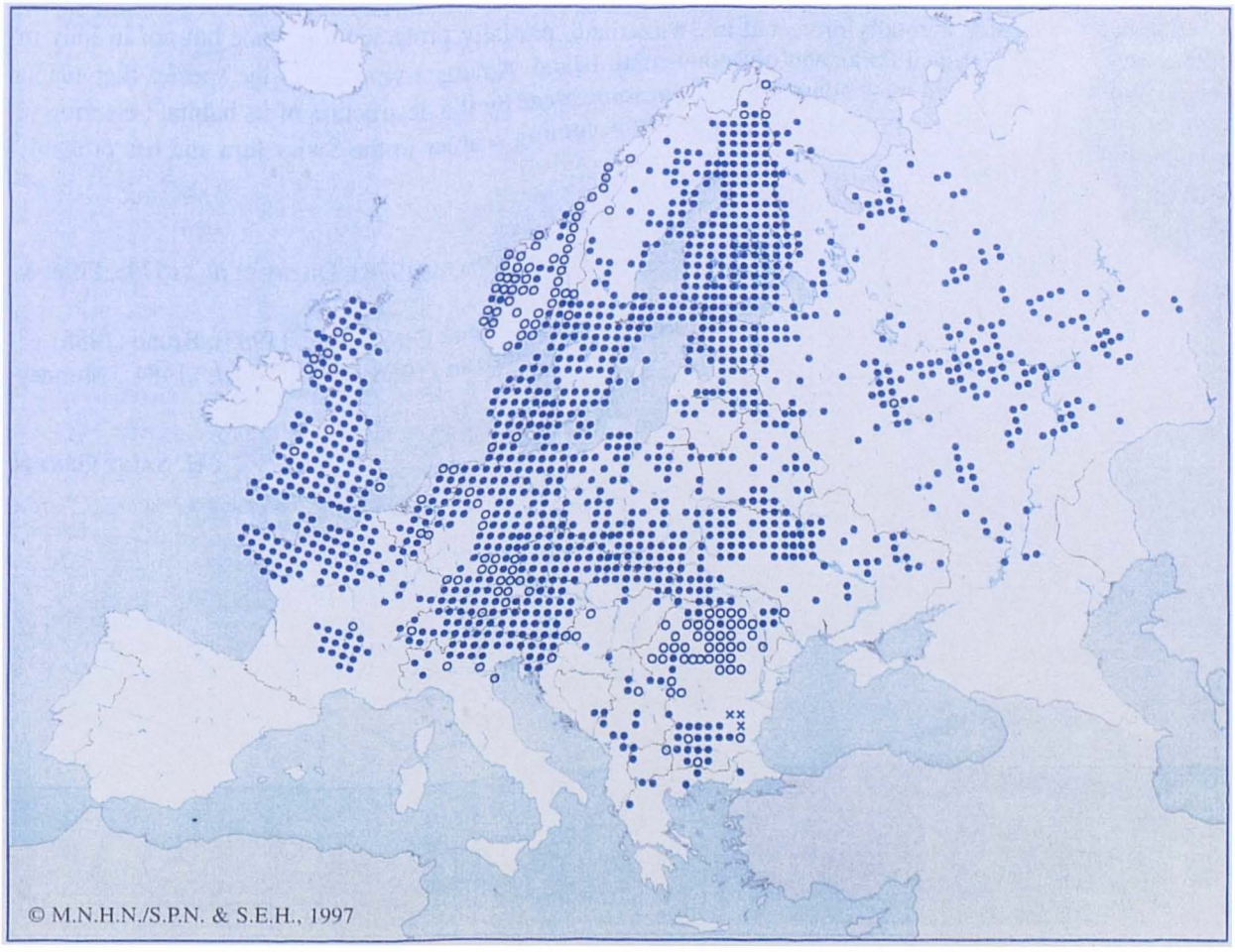


Figure 2.48: *V. berus* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

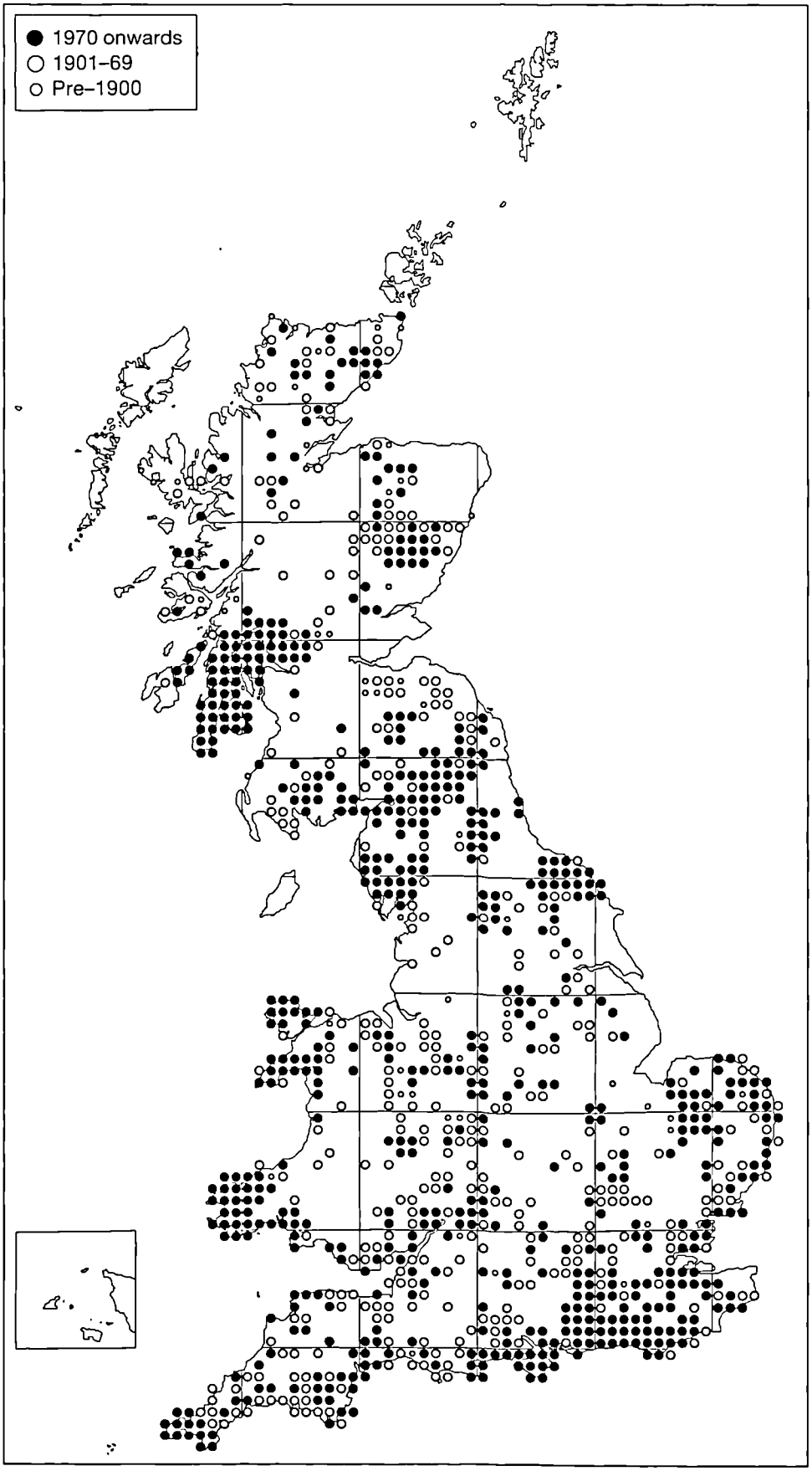


Figure 2.49: Distribution of *V. berus* in Britain (after Arnold, 1995).

It is similar in habits to other vipers, including *V. berus*, and is found in a variety of dry environments, from the perimeters of bogs to rocky hillsides (Saint Girons, 1997), and often in limestone areas (Street, 1979). It is commonly found in hilly and mountaineous districts, ascending to 2,500m in the Pyrenées, and 3,000m in the Alps (Arnold and Burton, 1978; Saint Girons, 1997; Street, 1979). It feeds mostly on small mammals, though occasionally on lizards and its venom is more potent than that of *V. berus*. In France, *V. aspis* is sympatric over a wide area with *V. berus* (Street, 1979), but where their ranges overlap, *V. aspis* tends to be restricted to warmer sunny locations at lower altitudes (Arnold and Burton, 1978).

Its distribution covers most of France, Italy, northeast Iberia and parts of the Alps (Arnold and Burton, 1978; Gasc *et al*, 1997). Its northern limit crosses from the mouth of the Loire to Paris (Saint Girons, 1997). It is present in the Moselle Valley, almost reaching Luxembourg at 49°N (Saint Girons, 1997). Fragmentary populations have only recently become extinct in southern Germany (Street, 1979). Like several other species considered here, *V. aspis* has apparently undergone a significant reduction in its Holocene range.

There are no fossil records for this species in Britain. Its range extends into northern France today, and it could be considered a potential Pleistocene colonist of the British Isles.

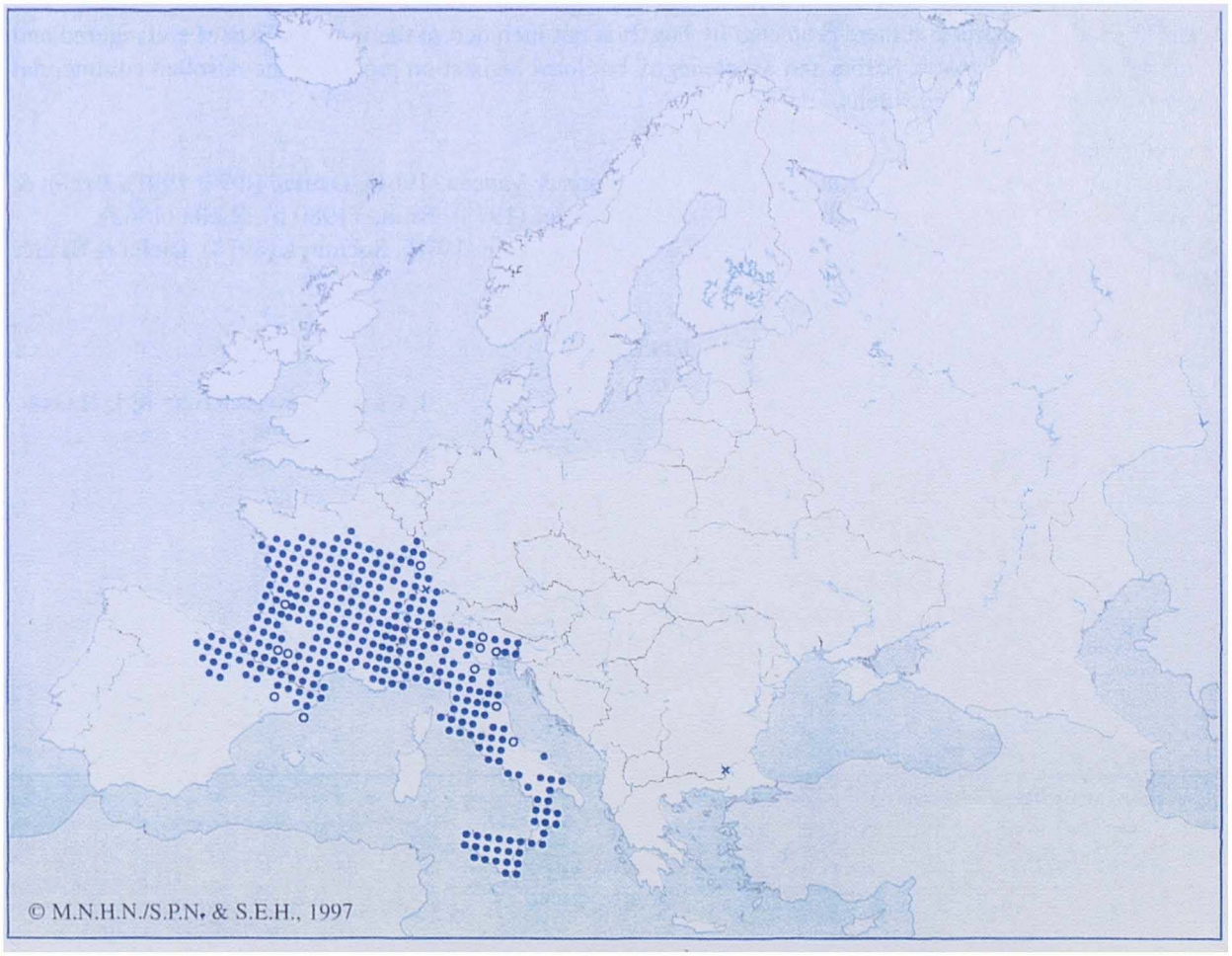


Figure 2.50: *V. aspis* (after Capula, 1990) and its distribution (after Gasc *et al*, 1997).

3 Literature review and critique of fossil herpetofaunas from the British Isles

3.1 Introduction

There has been much less published on British Quaternary herpetofaunas than on most other animal groups, for example, Mammalia, Mollusca and Coleoptera. Of the vertebrate groups, only avifaunas and icthyofaunas have suffered similar neglect. A. and E.T. Newton published a number of subfossil herpetofaunal finds between the 1860s and the 1920s, at a time when Victorian zoologists were prolific in their systematic descriptions of living organisms. Our understanding of Quaternary climatic change and chronological divisions has changed radically since then, and these early papers have little to offer modern Quaternary Science, other than noteworthy finds of exotics such as *E. orbicularis* (A. Newton, 1862; E.T. Newton, 1879).

Until recently, few fossil herpetofaunas have been published from the British Isles, though a large amount of material had been collected. As stated by Stuart (1982), 'Bones of frogs and toads are common fossils in small-vertebrate assemblages but no serious modern work has been done on Pleistocene Amphibia from the British Isles'. The problem is not only evident in Britain, as there are few European or other countries with well-described fossil herpetofaunas. Indeed, Sanchiz and Mlynarski (1979) remarked: 'Poland is possibly the only country in the world for which the whole record on amphibians and reptiles has been studied .... and where these data are continuously being updated.'

The lack of work on British fossil herpetofaunas has been addressed in recent years by J.A. Holman of Michigan State University. He has published over 20 papers, each dealing systematically with herpetofaunal material from a site, and usually discussing some biogeographical aspects and palaeoenvironmental inferences. His identifications include a number of exotic amphibian and reptile species, vindicating Stuart's (1982) assertion that 'Several species of snakes and lizards now exotic to the British fauna, would be expected to have occurred in England during interglacials....'. On the basis of work detailed in this thesis, some of Holman's identifications and diagnostic methods are considered unsatisfactory.

The Quaternary herpetofaunal material from the British Isles previously published is examined below in chronostratigraphic order, according to the supposed age of the site. Locations of sites with published herpetofaunal assemblages are shown in Figure 3.1. Both stage names and Oxygen Isotope stage numbers are used where appropriate. All illustrations provided by the original authors are reproduced in Figures 3.2 to 3.12. Identifications considered by the current author to be doubtful or uncertain are given in inverted commas. New assemblages studied by the author as part of this project are presented systematically in Chapter 6. There is still a vast amount of herpetofaunal material from the British Quaternary which has not been adequately studied, if at all, including that from a large number of Holocene archaeological sites.

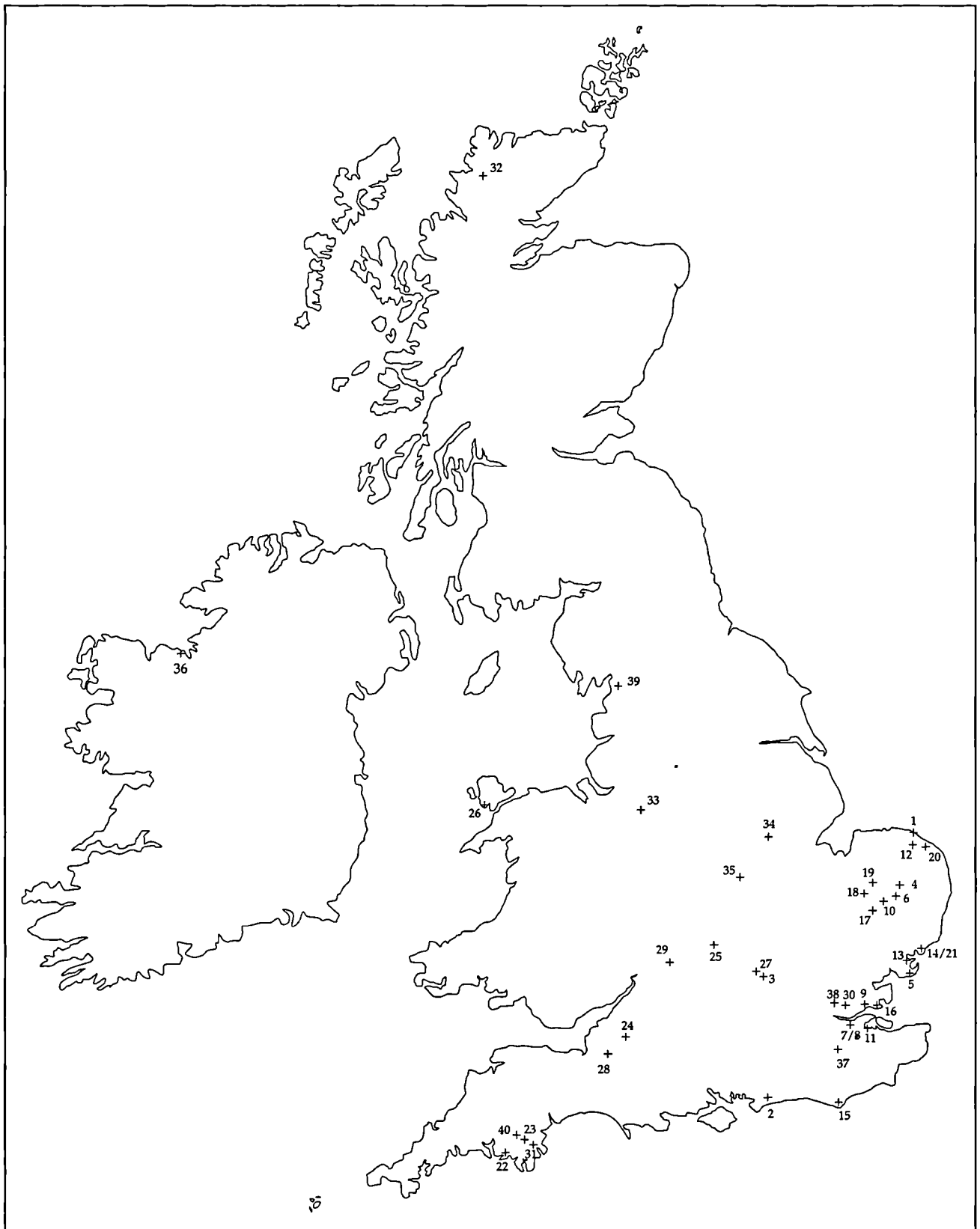


Figure 3.1: Locations of sites with published herpetofaunal assemblages.

3.2 Early Middle Pleistocene

The Early Middle Pleistocene (EMP) is used here to include sites correlated chronostratigraphically with stages older than Stage 11, but post-dating the Pastonian temperate stage. This begins with the Beestonian cold stage and ends with the cold stage traditionally believed to be represented by the particularly widespread Anglian glaciation. No herpetofaunal remains have yet been found in Quaternary sediments older than the Cromerian, and thus none older than the EMP. Several sites of EMP age have been examined for herpetofaunal remains. The chronostratigraphy and relative ages of these sites will be discussed in Chapter 8.

Herpetofaunal remains were first identified from the Cromerian type locality at West Runton, Norfolk, by E.T. Newton (1882a; 1882b) who listed *R. temporaria*, *R. esculenta*, *Bufo* sp., *T. cristatus*, *N. natrix* and *V. berus* (see Figure 3.2). The record of *T. cristatus* is probably incorrect. Newton (1882a) described a femur, but his illustration is of a humerus. From its shape, it also appears to belong to a smaller newt, of the *vulgaris* group, and Newton had not consulted comparative material of the smaller species. Newton also included this list in his '*The Vertebrata of the Pliocene Deposits of Britain*' (Newton, 1891). No further account had been published until Holman *et al* (1988) examined remains held in several museums and in J.D. Clayden's private collection. All of the most recently-collected material apparently came from Stuart's (1975) lower unit A of the Freshwater Bed, though no details of provenance appear to exist for Newton's earlier finds. The herpetofaunal remains described by Holman *et al* thus correspond with substages Cr Ib to IIb, a time of fully temperate woodland growth (West, 1980; Stuart, 1982; Holman *et al*, 1988). The collective herpetofauna given by Holman *et al* (1988) comprised *T. vulgaris*, *B. bufo*, *R. arvalis arvalis*, *R. esculenta* or *ridibunda*, *R. temporaria*, *A. fragilis*, *N. natrix* and *V.berus*. They also recorded *Triturus* sp., based only on Newton's (1882b) drawing, suggesting that Newton would have been unaware of other species of *Triturus*. Holman *et al* (1988) appear to have relied upon the illustrations from Böhme (1977) (who pleaded for caution in this difficult area), for their identification of *Rana*. Holman *et al*'s (1988) record of *N. natrix* may be safe from new material, but the record of *V. berus* was given on the basis that Newton's (1882b) illustration looked correct as the original material could not be traced. Holman (1989) described more material from West Runton, but without addition to the species list.

A few amphibian bones and one snake vertebra were recovered from EMP interglacial deposits at Sugworth, Oxfordshire (Stuart 1980; Holman, 1987a). One limb fragment of a salamandrid was thought not to belong to *Triturus* by Holman (1987a). If indeed this *is* a salamandrid limb bone, then it offers the intriguing possibility that perhaps another genus (e.g. *Salamandra*) *was* present in southern Britain during the EMP. Of the anuran remains found, most were indeterminate, but one ilium was listed by Holman (1987a) as *R. a. arvalis*. Though not qualified, this use of a subspecific name, as at West Runton (Holman *et al*, 1988), seems to refer to Böhme's (1977) drawings of the ilia of *R. a. arvalis* and *R. a. wolterstorfii*. Böhme (1977) did not describe the separation of the two subspecies, but provided drawings of their ilia. Stuart (1980)

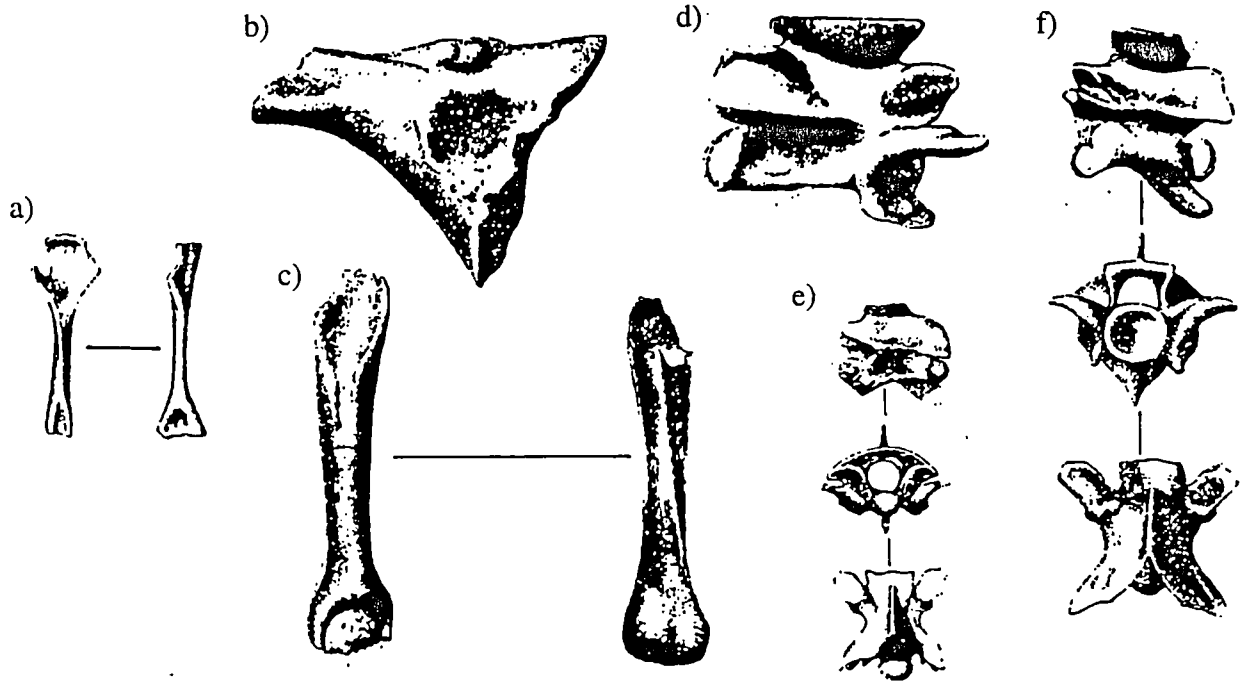


Figure 3.2: Herpetofaunal remains from the 'Forest Bed Series' (BM(NH) collection): a) humerus of '*T. cristatus*'; b) left ilium of '*Bufo* sp.'; c) right humerus of male *R. temporaria*; d) trunk vertebra of *N. natrix*; e) trunk vertebra of *V. berus*; f) trunk vertebra of *N. natrix* (after E.T. Newton, 1882).

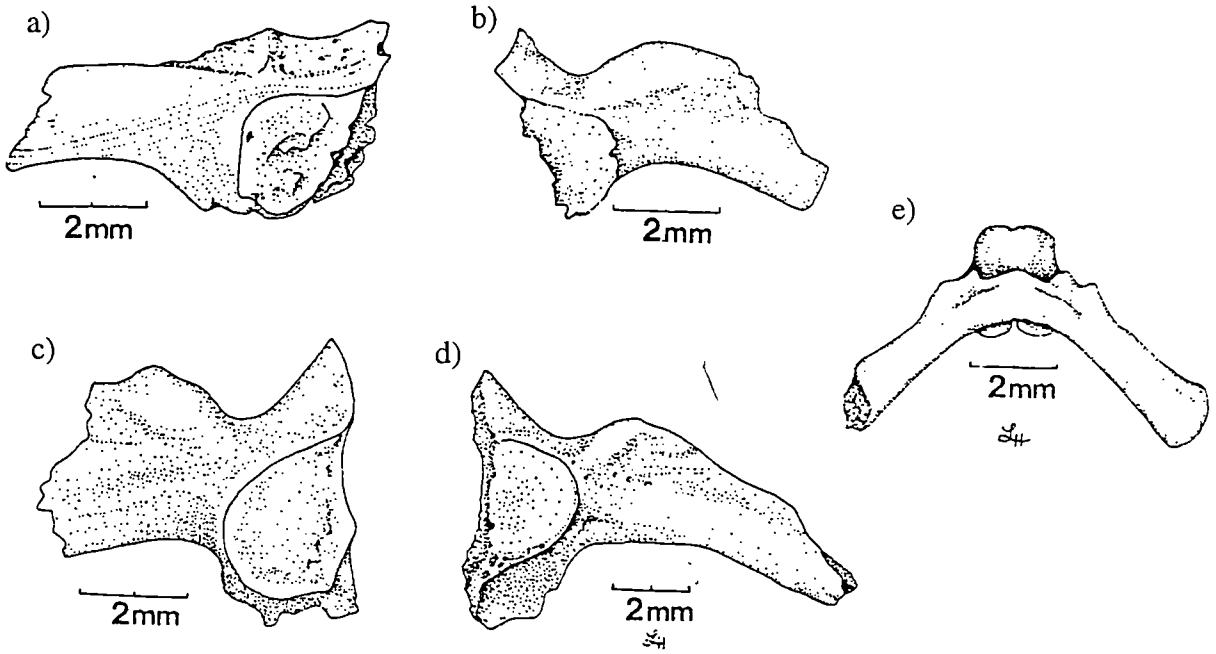


Figure 3.3: Anuran remains from West Runton (JC and BM(NH) collections): a) left ilium of *B. bufo*; b) right ilium of '*R. a. arvalis*'; c) left ilium of '*R. esculenta* or *ridibunda*'; d) right ilium of *R. temporaria*; e) sacrum of '*R. temporaria*' (after Holman *et al*, 1988).

identified two snake vertebrae as 'cf. *N.natrix*', but Holman (1987a) was unable to locate these and the record remains uncertain, but quite likely. Another snake vertebra from Sugworth was too fragmentary to be identifiable (Holman, 1987a). Gibbard *et al* (1997) also recorded undeterminate '*Bufo* sp. or *Rana* sp.' from EMP interglacial deposits at Broomfield near Chelmsford, Essex.

Lister *et al* (1990) described a vertebrate fauna from interglacial deposits at Little Oakley, Essex, which includes at least one anuran and two reptiles: *R. arvalis, Rana* sp., *Rana* sp./*Bufo* sp., *E. orbicularis, N. natrix*. This is the earliest record for *E. orbicularis* and it may provide a biostratigraphic correlation with Westbury Cave (see Chapter 8). The small herpetofauna from Little Oakley is indicative of temperate conditions. The thermal requirements for the breeding of *E. orbicularis* mean that its presence here is indicative of July temperatures at least 2-3 ^{o}C warmer than today in southern Britain (Isberg, 1929; Stuart, 1979). This fauna also fits with other palaeoecological evidence (Gibbard and Peglar, 1990; Preece, 1990) from the site.

The excavations at Eartham Pit, Boxgrove, West Sussex, which produced hominid and other mammalian remains, also produced a rich herpetofaunal assemblage. The deposits clearly belong to an interglacial phase of the EMP, though probably not the Cromerian *sensu stricto* (Roberts *et al*, 1986). Their age is discussed in Chapter 7. The assemblage listed by Holman (1992a) is as follows: *T. helveticus, T. helveticus/vulgaris, Triturus* sp., *P. fuscus, B. bufo, B. calamita, Bufo* sp., *R. arvalis, R. temporaria, Rana* sp., *A. fragilis, Lacerta* cf. *L. vivipara, N. natrix* and *Natrix* sp. All of the amphibian and reptile remains came from units 4 - 6, and mostly from unit 4c of the Upper Slindon Sands (Roberts *et al*, 1986; Holman, 1992a). Much of this material was recently re-examined, resulting in significant changes to the species list. The revised identifications are detailed in Chapter 6.

Vertebrate-rich cave-fill deposits, dating to an EMP interglacial stage, were exposed during quarrying of the Carboniferous Limestone near Westbury-sub-Mendip, Somerset (Bishop, 1982; Andrews, 1990). The stratigraphy is evidently much more complex than was at first imagined, and the relationships between laterally discontinuous sequences are uncertain (Currant, pers. comm., 1997).

Stuart (1979) recorded a carapacial fragment of *E. orbicularis* from the site, and offered biostratigraphic comments on the age of the deposits, noting their complexity and difficulties in correlation. A rich herpetofaunal assemblage was later identified by Holman (1993a): *P. punctatus, R. temporaria, Rana* sp., *E. orbicularis, A. fragilis, C. austriaca, N. natrix, Natrix* sp. and *V. berus* (see Figure 3.5). The record of *E. orbicularis* is based on Stuart's (1979) identification. The record of *P. punctatus* is the first from Britain. The record of *C. austriaca* is also worthy of note as the earliest known presence of this species, the rarest British reptile.

All herpetofaunal remains came from the side chamber of Westbury Cave (Holman, 1993a), cf. 'western end' of Stringer *et al* (1996). The stratigraphic system adopted by Bishop (1982) contained herpetofaunal remains as follows: Unit 8 - *E. orbicularis* and *C. austriaca*; Unit 11 - *P. punctatus, R. temporaria* and *Rana* sp.; Unit 12 - *R. temporaria, Rana* sp., *V. berus*; Unit 13 - *P.*

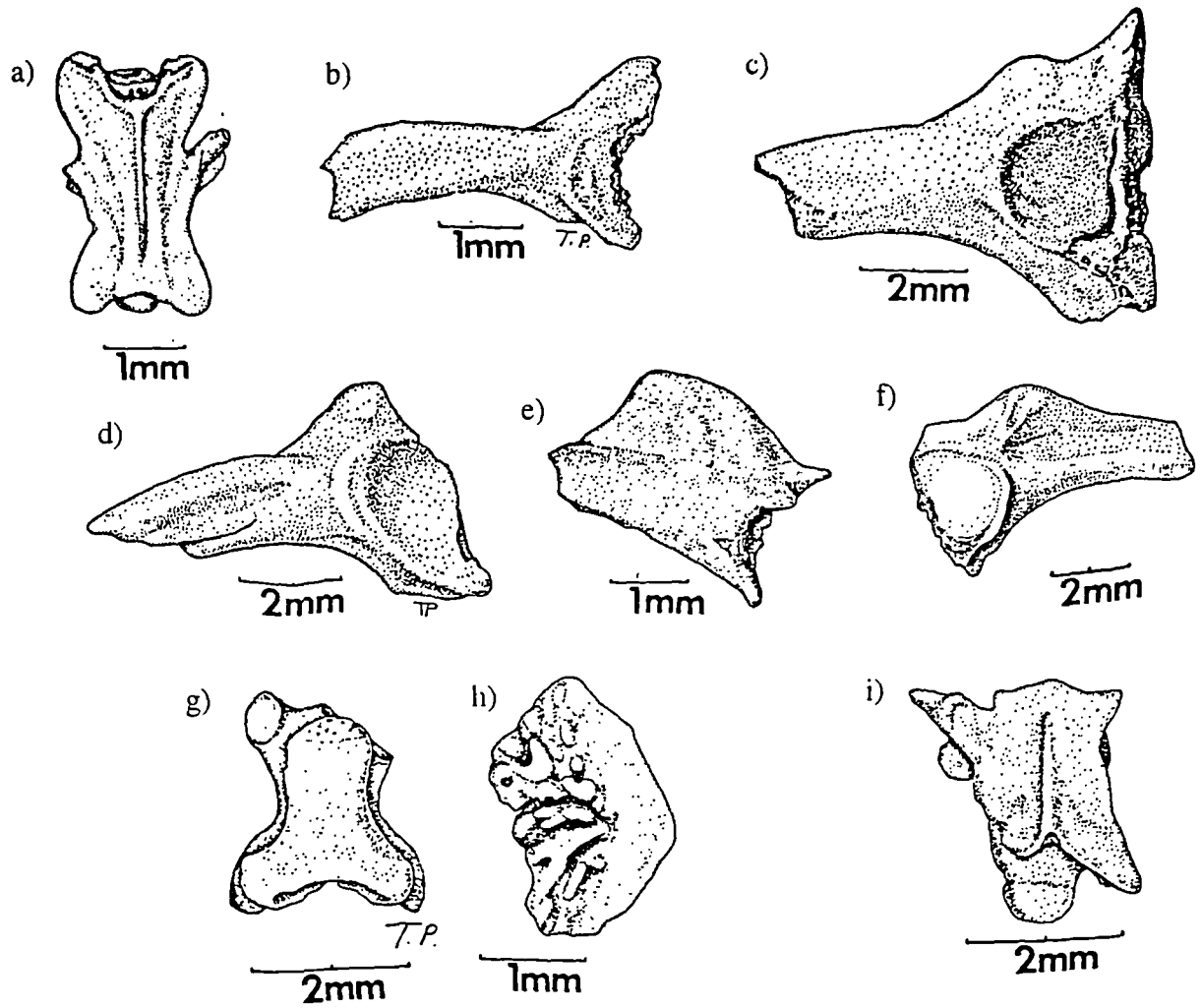


Figure 3.4: Herpetofaunal remains from Boxgrove (NHM), 2mm scale bars (some identifications have been modified, see Chapter 6.1): a) trunk vertebra of *T. alpestris*, illustrated as '*T. vulgaris*' by Holman (1992a); b) left ilium of *P. fuscus*; c) left ilium of *B. bufo*; d) left ilium of *B. calamita*; e) left ilium of *R. arvalis*; f) right ilium of *R. temporaria*; g) trunk vertebra of *A. fragilis*; h) osteoderm of *A. fragilis*; i) trunk vertebra of cf. *Vipera* sp., identified as '*Natrix* sp.' by Holman (1992a) (after Holman, 1992a).

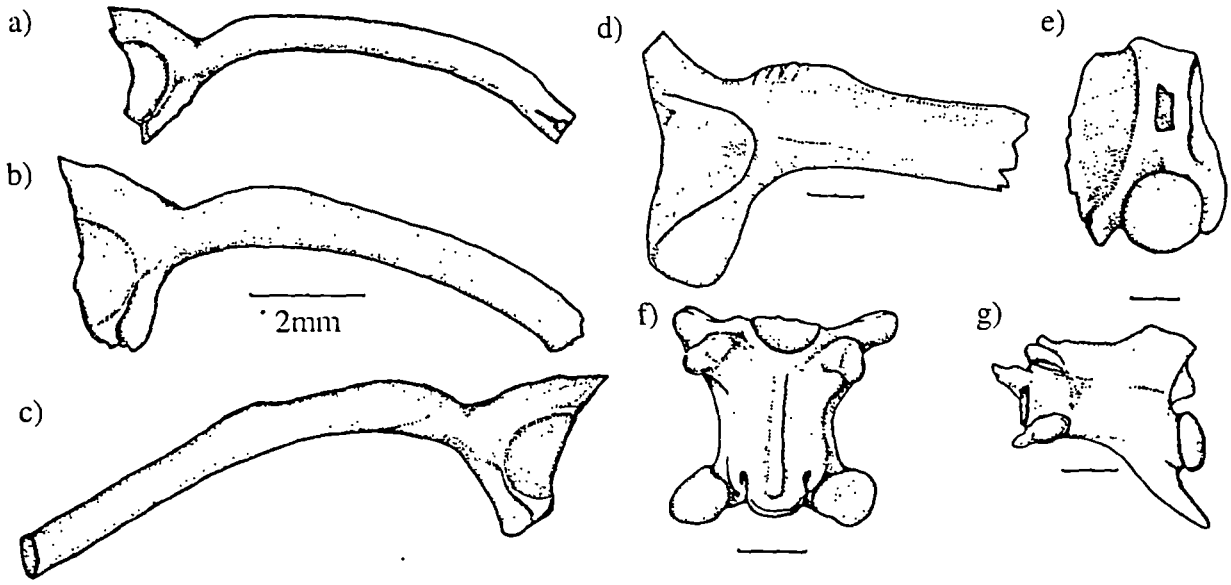


Figure 3.5: Herpetofaunal remains from Westbury-sub-Mendip (BM(NH) collection), 2mm scale bars: a) right ilium of *P. punctatus*; b) right ilium of *P. punctatus*; c) left ilium of *P. punctatus*; d) right ilium of *R. temporaria*; e) left humerus of *Rana* sp.; f) trunk vertebra of *C. austriaca*; g) trunk vertebra of *V. berus* (after Holman, 1993).

punctatus, R. temporaria, Rana sp., *N. natrix* and *Natrix* sp; Unit 14 - *N. natrix* and *Natrix* sp.; Unit 15 - *Rana* sp., *A. fragilis, N. natrix, Natrix* sp. and *V. berus*. The lowest unit (corresponding with mammal fauna 2 of Bishop, 1982) contained the two most thermophilous species found: *E. orbicularis* and *C. austriaca*. The five upper units are separated from the lower fauna by 4.5m of breccia, devoid of herpetofaunal remains. The herpetofauna of the upper units is of interglacial character. The two herpetofaunas are very different, and support lithostratigraphical and small mammal evidence (Andrews, 1990; Stringer *et al*, 1996) for two distinct interglacials.

At Hall's Pit, near Benson in Oxfordshire, cryoturbated fluviatile gravels with ice-wedge casts, form part of the Wallingford Fan Gravels. These probably date to the Anglian, but might be younger (Horton and Whittow, in Shephard-Thorn and Wymer, 1977; Stuart, 1982). The rare vertebrate remains included arctic mammals such as *L. lemmus* but also anurans, identified by A. Horton as 'frog *Rana* sp. and/or toad *Bufo* sp.' (Stuart, 1982). If these remains belong to a glacial cold stage, then the likelihood is that they are *R. temporaria*, which lives today at the margins of alpine glaciers, and even in meltwater pools. This is the oldest cold-stage record of any amphibian or reptile from the British Isles.

Holman (1993c) discussed the probable asynchroneity of the EMP herpetofaunas, referring to 'earlier Cromerian' and 'later Cromerian' faunas, but did not attempt any biostratigraphic division of herpetofaunal assemblages.

3.3 Late Middle Pleistocene

The Late Middle Pleistocene (LMP) is used here to describe the period after the Anglian, including all temperate and intervening cold stages up to the beginning of the Ipswichian. This is perhaps the most contentious part of the Pleistocene, and an accepted chronology has not been established. Until the 1970's, it was thought that only one LMP interglacial (the Hoxnian) occurred (Mitchell *et al*, 1973). It is now generally accepted that there were at least three temperate stages over this timespan. Sites previously attributed to the orthodox Hoxnian are now thought to fall into two distinct categories: Stage 11 and Stage 9. In addition, the most contentious of all has been the acceptance of a Stage 7 interglacial. This has required the reconsideration of many Ipswichian sites. The post-Hoxnian cold stage, the Wolstonian, has also been the subject of much debate. The timeslot it fills is effectively divided into two cold-stages by the addition of a Stage 7 interglacial. Thus, the LMP is here taken to mean the period lasting from Stage 11 to Stage 6. The latter precedes the thermal maximum of the Ipswichian interglacial (Substage 5e).

Organic deposits at Cudmore Grove, Mersea Island, Essex, contain the largest herpetofauna known from the British Isles. The fourteen species include seven which are exotic, and provide evidence of an interglacial climate interpreted by the authors as having milder winters and warmer summers than today (Holman *et al*, 1990). An alternative interpretation is presented in Chapter 8. The estuarine deposits, which were laid down in a deep channel cut into the Eocene London Clay and overlain by Mersea Island Gravel, were exposed by coastal erosion on the foreshore during

1987 (Bridgland *et al*, 1988). The sedimentary sequence begins with a marine regressive layer (Bed 2 of Bridgland *et al*, 1988) with a brackish mollusc and ostracod fauna, giving way to a mostly freshwater unit (Bed 3) from which the rich herpetofaunal assemblage came (Holman *et al*, 1990). This unit also yielded an abundant small mammal assemblage, larger vertebrates including beaver (*Castor fiber*) and macaque (*Macaca sylvanus*), and freshwater molluscs; most notably the thermophile *Corbicula fluminalis* (Bridgland *et al*, 1988). The herpetofaunal list (Holman *et al*, 1990) is as follows: *T. cristatus, T. vulgaris, Triturus* sp., *Hyla* sp, *B. bufo, R. arvalis, R. esculenta* or *ridibunda, R. lessonae, Rana* sp, *E. orbicularis, A. fragilis, Lacerta* sp., *N. natrix, N. maura* or *tessellata, Natrix* sp., *E. longissima, V. berus*. The record of *Hyla* sp is from a humerus, which is not specifically diagnostic: neither of the two European species are indigenous today. As at Boxgrove and Barnham, *R. arvalis* is recorded from Cudmore Grove. The addition to the frog fauna of two green frog species is, however, very noteworthy. The identification of green frogs from their ilia is notoriously difficult (e.g. Böhme, 1977; Böhme and Günther, 1979; Gleed-Owen and Joslin, 1996), and this material should ideally be re-examined. The identification of *R. lessonae* is based upon a fragmentary ilium (Figure 3.6d). The drawings of *R. esculenta* or *ridibunda* (Figure 3.6e,f) are less convincing and appear more likely to be *R. arvalis* ilia. *E. orbicularis* is represented at Cudmore Grove by four carapacial and plastral fragments. This record suggests a warmer summer temperature than that today for Essex. The vertebrae assigned to *N. maura* or *tessellata* could not be specifically identified (Holman *et al*, 1990). The illustrated trunk vertebra labelled as '*N. natrix*' (Holman *et al*, 1990) has anteriorly-directed prezygapophyseal processes, and probably belongs to *N. maura* or *tessellata.* These species have western and eastern distributions, respectively, and together with *E. longissima*, do not reach northern Europe. Holman *et al* (1990) discussed the palaeoclimatic and zoogeographic implications of the herpetofauna, in relation to its assumed age of Ho IIIb. They noted that the pollen data and mammals such as *Macaca sylvanus, Castor fiber, Capreolus capreolus* and *Apodemus sylvaticus* indicated a wooded local environment, but that *E. longissima* suggested dry scrubby conditions in the vicinity. They interpreted summer temperatures as being in excess of 17-18°C based on the modern tolerances of *E. orbicularis.* In addition, they noted that *E. longissima* does not reach as far north as *E. orbicularis* in the east of its range. It was suggested that this indicates milder winters than today and offered an oceanic climatic reconstruction. However, Holman *et al* (1990) noted that *R. arvalis* gave a conflicting interpretation to that given by the rest of the herpetofauna.

Deposits at East Farm, Barnham, Suffolk, have produced a very promising array of small vertebrate remains (Ashton *et al*, 1994). Most of the material came from calcareous silt and clay horizons lying above the Anglian Lowestoft Till, and are interpreted as representing interglacial conditions immediately after the Anglian cold stage. J.A. Holman identified the herpetofauna, though only a brief summary was included in the report by Ashton *et al* (1994). No systematic information was given, but the species list is as follows: *T. cristatus, T. helveticus, T. vulgaris, H. arborea, B. bufo, B. calamita, R. arvalis, R. temporaria, E. orbicularis, A. fragilis, E. longissima*

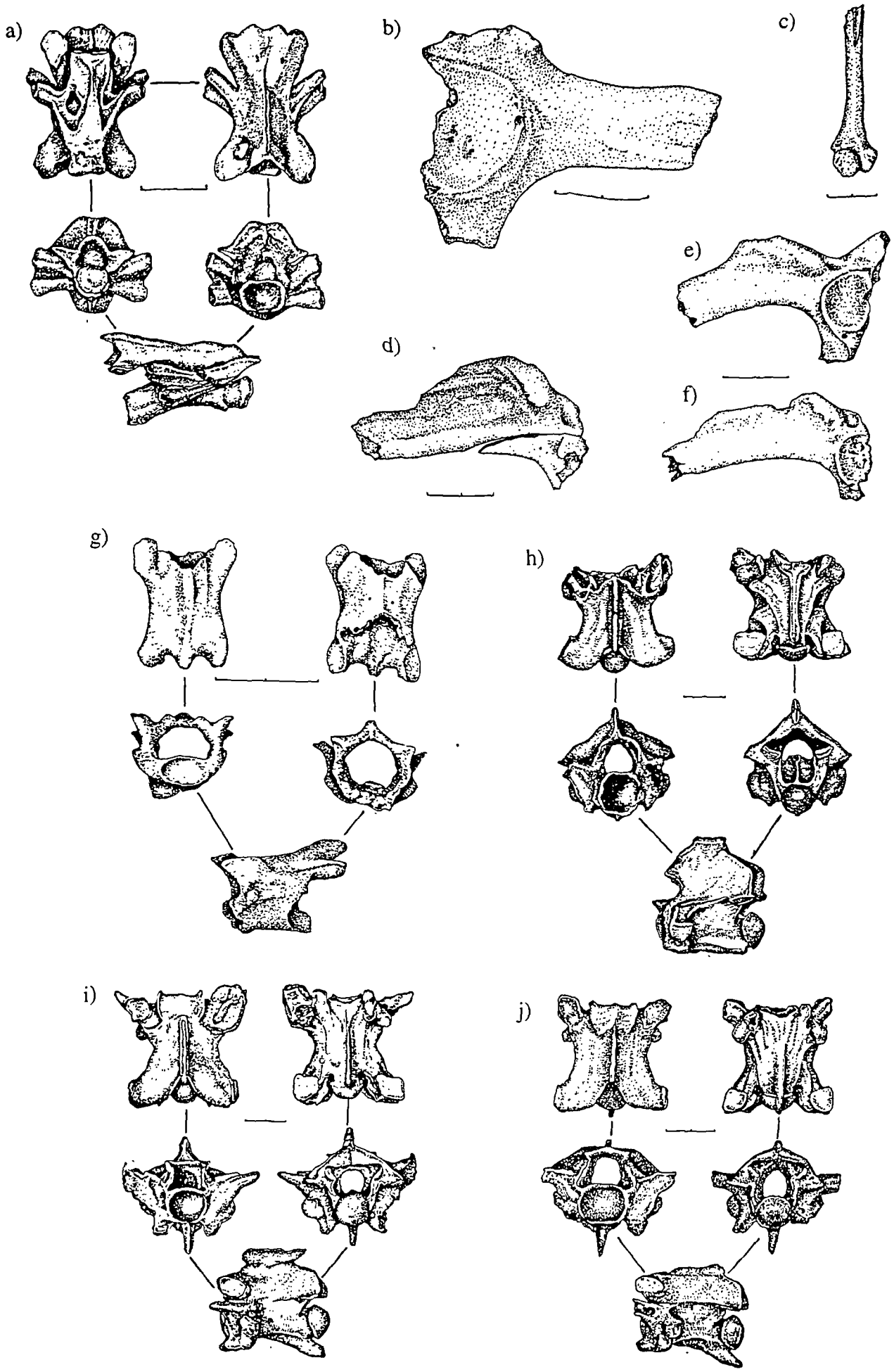


Figure 3.6: Herpetofaunal remains from Cudmore Grove (JC collection), 2mm scale bars: a) trunk vertebra of *T. cristatus*; b) right ilium of *B. bufo*; c) right humerus of *Hyla* sp.; d) left ilium of '*R. lessonae*'; e) left ilium of '*R. esculenta* or *ridibunda*'; f) left ilium of '*R. esculenta* or *ridibunda*'; g) trunk vertebra of *Lacerta* sp.; h) trunk vertebra of *E. longissima*; i) trunk vertebra of *N. natrix*; j) trunk vertebra of *V. berus* (after Holman *et al.* 1990).

and *N. natrix*. *H. arborea*, *E. orbicularis* and *E. longissima* give a comparable picture to that of Cudmore Grove. Ashton *et al* (1994) also inferred from the presence of *E. orbicularis* that mean July temperatures in East Anglia must have been warmer than today, at least 17 or 18°C.

Holman (1994) gave brief details of a small herpetofauna from Beeches Pit, West Stow, Suffolk. This is most notable for its inclusion of two vertebrae of *E. longissima*. There are now three records for this snake species, which has not been recorded from any other part of the Pleistocene. Thus it may have biostratigraphic significance. The other remains from Beeches Pit were of *Triturus* sp., *Rana* sp. and *A. fragilis*. The presence of *E. longissima* appears to equate with the Cudmore Grove and Barnham faunas.

Holman (1987b) described a few remains of *B. bufo* from Barnfield Pit, Swanscombe, Kent. These consisted of associated skeletal parts in a small block of sandy matrix. The exact provenance of the herpetofaunal remains within the stratigraphic scheme of Ovey (1964) was not given. The lithology is a series of sands, silts and gravels deposited in a broad channel, probably cut by an early Thames. The site is well known for its human skull discovery. No other herpetofaunal remains have been identified from Swanscombe.

Some herpetofaunal remains were recovered from Dierden's Pit, Ingress Vale (close to Barnfield Pit) Swanscombe, Kent. The remains consist of a carapacial fragment of *E. orbicularis* (Figure 6 in Stuart, 1979), and undetermined frog or toad remains (Stuart, 1982). Holman (1987b) also identified several *N. natrix* vertebrae from the site, but did not study the amphibians. These are as yet unidentified, and further examination would be useful. The site produced an abundance of other vertebrate remains, which are similar to those from Swanscombe, except for the inclusion of *T. cuvieri* which is characteristic of Hoxne and Clacton (Stuart, 1982).

At Hoxne in Suffolk, the Hoxnian type site occupies a lacustrine basin cut into Anglian cold stage gravels (Stuart, 1982). Sparse herpetofaunal remains from the organic deposits were identified by Holman (1993b) as *B. bufo, Bufo* sp, *N. natrix* and *Natrix* sp. The impoverished nature of this assemblage is very likely to be a function of taphonomy, rather than a true representation of the herpetofauna of Stage 9, as a lake basin is not the ideal location for the accumulation of small vertebrate remains. The stratigraphic sequence at Hoxne was described in detail by West (1956), who assigned pollen zones which have subsequently been used for the correlation of other LMP sites. The large vertebrate fauna is less diverse than that of Swanscombe, and includes the extinct giant beaver *Trogontherium cuvieri* (Stuart, 1982).

Riverine deposits at Greenlands Pit, Purfleet (Essex), yielded an interglacial molluscan and fish fauna, and herpetofaunal remains (Snelling, 1975; Holman and Clayden, 1988; Holman, 1995b). A fluvial connection to the sea was indicated by brackish sediments reported by Allen (1977) and by eel and sturgeon identified by A. Wheeler (Holman and Clayden, 1988). The herpetofaunal list includes at least six species: *T. cristatus, Triturus* sp., *B. bufo, R. a. arvalis, R. temporaria, Rana* sp., *A. fragilis* and *Natrix* cf. *N. natrix*. Only *R. a. arvalis* is not native to Britain today. The record of *N. natrix* is tentative, but seems very reasonable in a temperate riparian

environment.

Hallock *et al* (1990) described a herpetofauna from Itteringham, Norfolk. The deposits are detritus muds which underly cold stage gravels, and display an interglacial character. An Ipswichian age was tentatively assigned by the authors, but it is now believed that the deposit have a Stage 7 age (Currant, 1989; Schreve, 1998). According to the authors, the collective vertebrate fauna (mammals, birds, fish, amphibians and reptiles) suggest a mean summer temperature at least 2-3°C warmer than today. The herpetofaunal list is a follows: *B. bufo, Bufo* sp., *Hyla* sp., *R. esculenta* or *ridibunda, R. temporaria, Rana* sp., *E. orbicularis* and *N. natrix*. Holman (1992b) identified the *Hyla* ilium as *H. meridionalis* which has a southwest European range today, and is the most southerly species recorded from the British Pleistocene. It is also the most thermophilous, and is accociated with warm winters (García París, 1997). It is interesting that *H. meridionalis* rather than *H. arborea* was found at Itteringham, indicating that its range was then much more extensive. Collectively, this is a notably thermophilous fauna, and is the most diverse assemblage recovered from a Stage 7 site. As interpreted by Hallock *et al*, the herpetofauna suggests a local environment of marshy river margin or weedy pond. All the amphibian species would breed in a low-energy water body, and both reptile species would hunt in it.

Stuart (1979) recorded a plastral fragment of *E. orbicularis* from Selsey, West Sussex, and Holman (1992d) listed some additional elements: *B. bufo, B. calamita, Rana* sp. and *N. natrix*. These authors accorded with West and Sparks (1960) who suggested an Early-temperate (Ip Ib-IIb) Ipswichian age for the site (Stuart, 1979). Allen *et al* (1996) suggested the possibility that it may belong to Stage 7. However, based on recent studies, Holman's (1992d) identification of *B. calamita* from Selsey may be erroneous. The *Rana* identification is from a partial femur only, and the *N. natrix* identification is from a fragmentary vertebra. The presence of *E. orbicularis* is notable, however, though it was not found in association with the material described by Holman (1992d). Stuart (1979) suggested that *E. orbicularis* could quite easily burrow into exposures of older temperate deposits, but its presence in a fully temperate Stage 7 does not require this explanation.

Stoke Tunnel (Ipswich, Suffolk) and Harkstead (Suffolk) have produced *E. orbicularis*, and were believed to belong to the Ipswichian by Stuart (1979). It has since been suggested that both sites are of Stage 7 age (Wymer, 1985).

Cold-stage records from the LMP are as sparse and non-specific. Holman (1995) identified *R. temporaria* and *Rana* sp. from Baker's Hole Pit, Northfleet, Kent. Stratigraphically, the site is Wolstonian (Stuart, 1982), and the associated large mammal fauna of *M. primigenius, E. ferus* and *C. antiquitatis* suggests a periglacial climate (Jones and Keen, 1993). Stuart (1982) recorded 'frogs and/or toads' from Waterhall Farm, Hertfordshire, and recorded the same from the Glutton/Bear Strata of Tornewton Cave, Devon. Holman (1990) subsequently identified one ilium from Tornewton Cave as *R. temporaria*, attributing it to a Wolstonian level. Considering that Currant (1996) believed that the Bear Stratum might be of Substage 5e age, it can only be assumed that

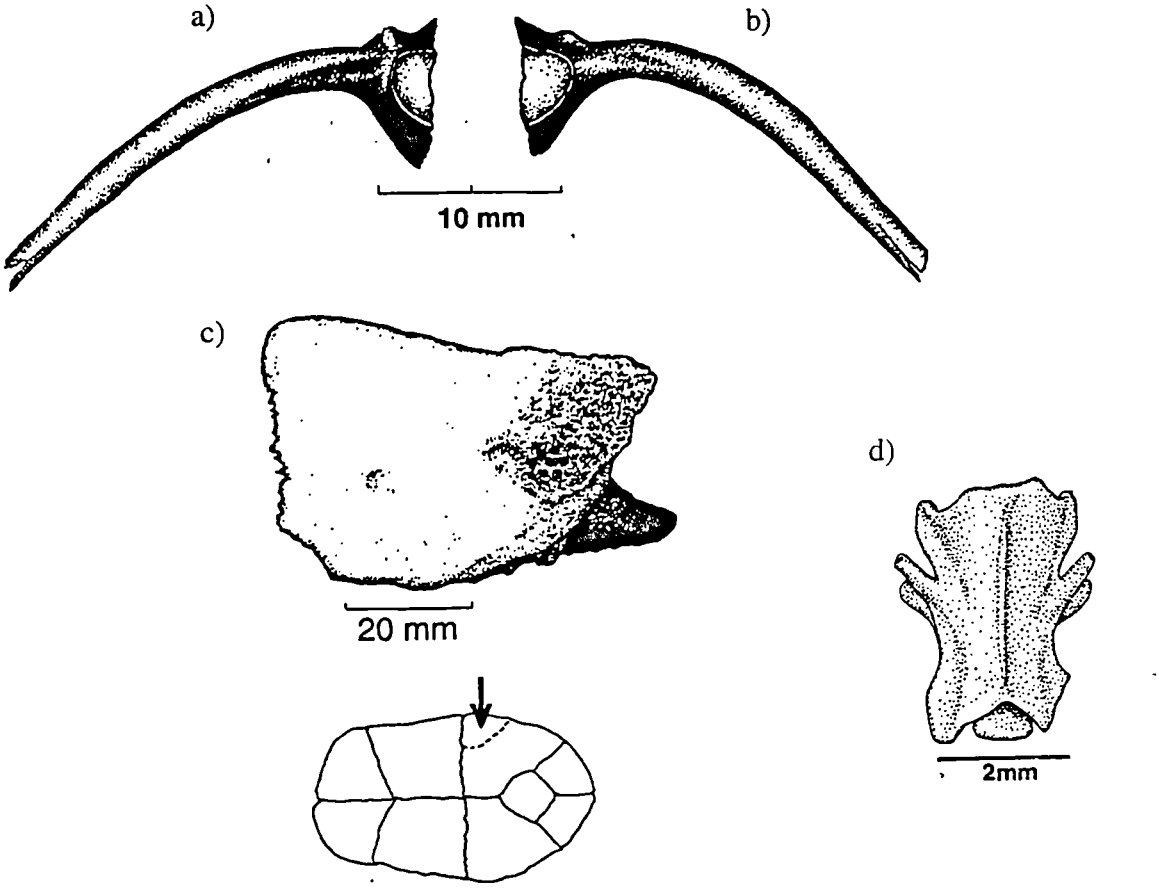


Figure 3.7. Herpetofaunal remains from Selsey (Holman in possession of material): a) left ilium of '*B. calamita*'; b) right ilium of *B. bufo*; c) partial right hyoplastron of *E. orbicularis*', and Purfleet (Holman, 1995): d) trunk vertebra of *T. cristatus* (after Holman, 1991).

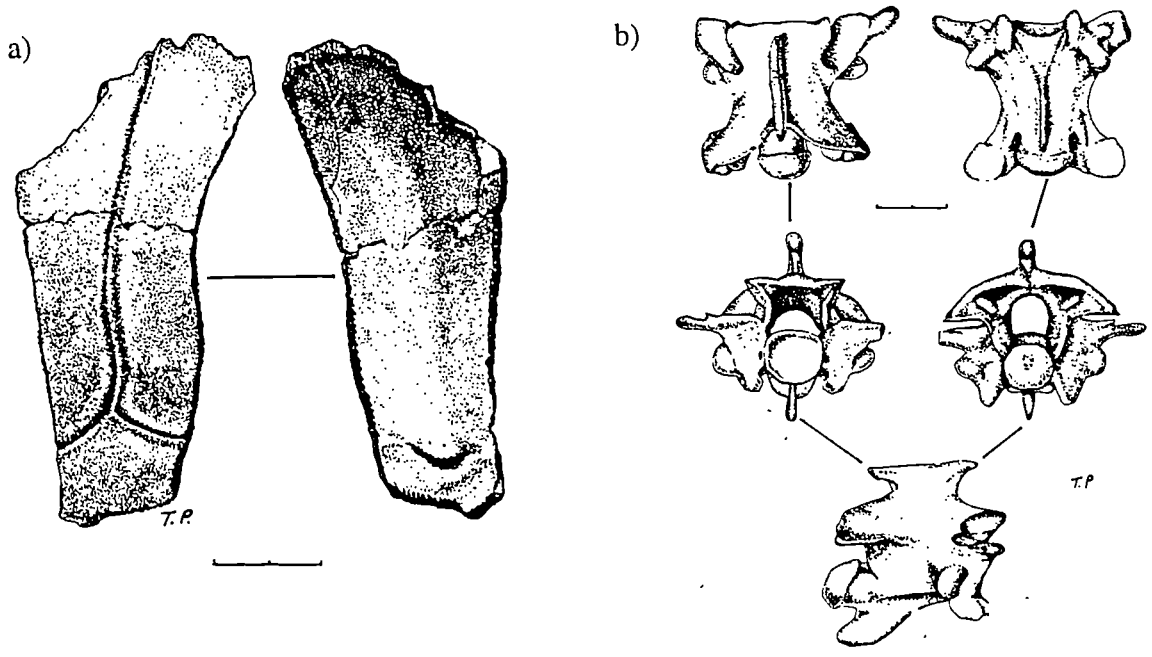


Figure 3.8: Reptile remains from Shropham (JC collection), 2mm scale bars: a) 2nd left pleural (costal) of *E. orbicularis*; b) trunk vertebra of *N. natrix* (after Holman and Clayden, 1990).

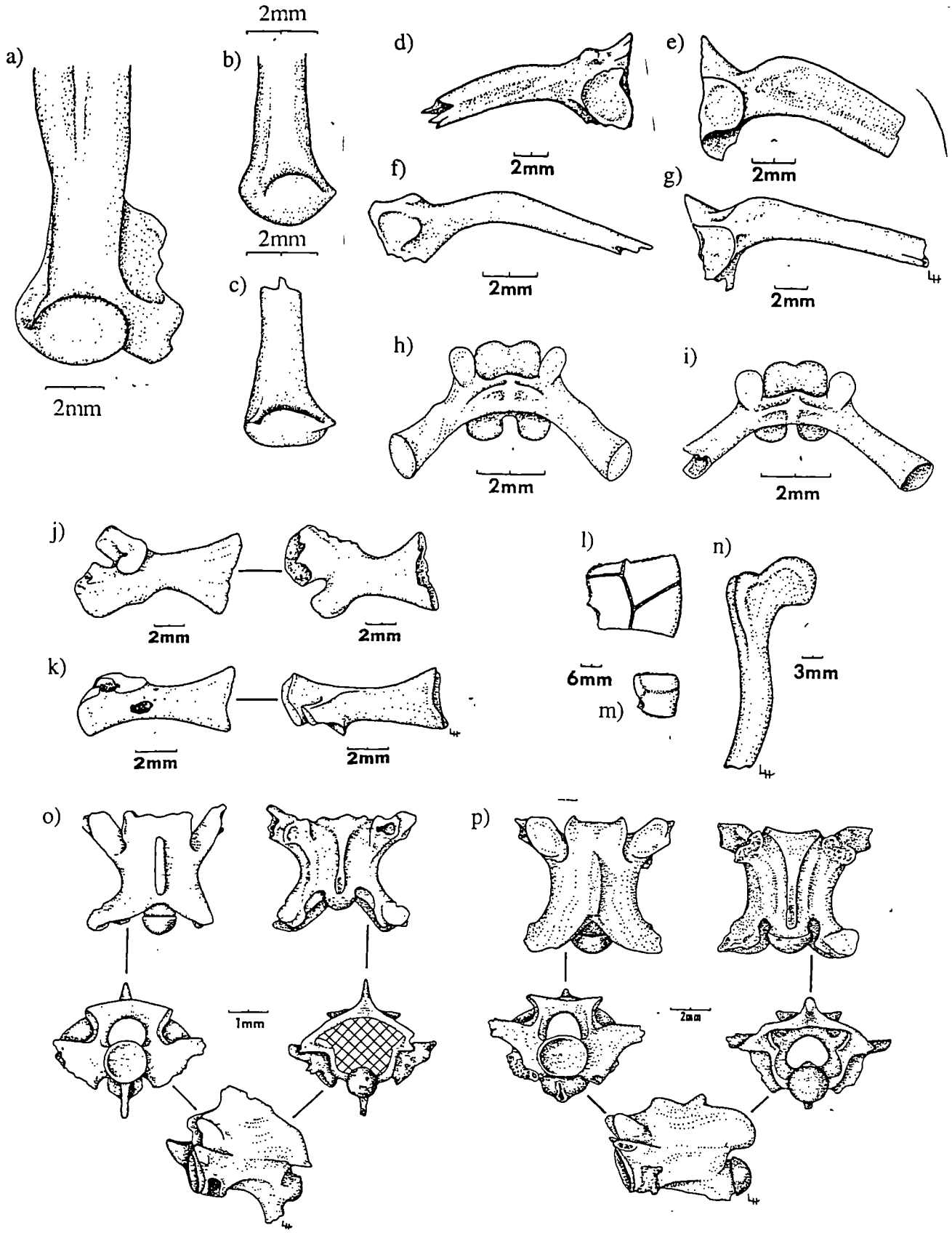


Figure 3.9: Herpetofaunal remains from Itteringham (JC and CM collections): a) left humerus of *Rana* sp.; b) humerus of *Rana* sp.; c) humerus of *Bufo* sp.; d) left ilium of *B. bufo*; e) right ilium of '*R. esculenta* or *ridibunda*'; f) right ilium of '*H. meridionalis*'; g) right ilium of *R. temporaria*; h) sacrum of '*R. temporaria*'; i) sacrum of '*R. esculenta* or *ridibunda*'; j) left scapula of *Bufo* sp.; k) left scapula of *Rana* sp.; l) 3rd left peripheral of *E. orbicularis*; m) 2nd left peripheral of *E. orbicularis*; n) right humerus of *E. orbicularis*; o) cervical ('anterior trunk') vertebra of *N. natrix*; p) trunk vertebra of *N. natrix* (after Hallock *et al*, 1990; Holman, 1992).

Holman's identification is on material from either the Glutton or Bear Strata.

3.4 Late Pleistocene (except Devensian Lateglacial)

Four sites of Ipswichian age *sensu stricto* have produced herpetofaunal remains. Newton (1879) described and illustrated a partially intact shell from the 'Mundesley River Bed'. Based on palynological evidence, the associated deposits are believed to belong to the Last Interglacial: zones Ip Ib to early Ip IIb (Stuart, 1979). The mostly articulated pieces of carapace and plastron (Figure 3.10) appear to belong to one individual; the remains are kept in the NCM collections. Stuart (1979) also described *E. orbicularis* remains from Bobbitshole (Ipswich, Suffolk) and Swanton Morley (Norfolk).

Non-*Emys* herpetofaunal remains have been recorded from three Ipswichian sites: Swanton Morley, Shropham and Itteringham. The riverine sediments at Swanton Morley, Norfolk, appear to span pollen subzones Ip Ib to IIb of the Last Interglacial (Coxon *et al*, 1980). As is typical of true Ipswichian sites, the remains of *Hippopotamus amphibius* indicate a warmer climate than that of today (Stuart, 1976). This reconstruction was supported by fruits of *Trapa natans* (water chestnut) from Ip IIb sediments, and remains of *E. orbicularis* from Ip IIa (Coxon *et al*, 1980). Holman (1987a) identified the following amphibians and reptiles: *B. bufo, R. a. arvalis, R. temporaria, Rana* sp., *E. orbicularis* and *N. natrix*.

A larger herpetofauna from Shropham, Norfolk, was described by Holman and Clayden (1990), though the geology and stratigraphic details of the site have yet to be published. The deposits are organic muds lying beneath around 8m of Devensian gravels and mud lenses. The herpetofaunal list is as follows: *T. vulgaris, B. bufo, R. arvalis, R. temporaria, Rana* sp. (green frog), *Rana* sp., *E. orbicularis, Lacerta* cf. *L. vivipara, N. natrix, Natrix* cf. *N. maura* or *tessellata* and *Natrix* sp. This includes the interesting additions to Ipswichian herpetofauna of *T. vulgaris* and a small lizard, which may be *L. vivipara*. Again, *Emys* indicates a warmer climate than today. The green frog remains, *R. arvalis,* and the continental natricine snake all fit with a picture of a southern modern analogue. The remains came from two different parts of the pit, and therefore perhaps from stratigraphically different layers relating to different zones of the Last Interglacial.

Herpetofaunal remains have been reported from a few sites of post-Ipswichian, pre-Devensian Lateglacial age, though not in great detail and without firm dating. Devensian Lateglacial herpetofaunas are grouped and discussed in the Holocene section below. They are more closely allied, both faunally and temporally, to the amphibians and reptiles of the last 10,000 years.

Holman (1992e) described two separate horizons of organic mud within the Devensian gravels at Shropham: 'Pocket 1/Shropham D' and 'Pocket 2'. Pocket 1 contained *R. temporaria* and *Rana* sp. (Holman, 1990; 1992e) and Pocket 2 produced *R. temporaria* and *N. natrix* (Holman, 1992e). These may or may not represent the same episode, but the presence of *N. natrix* in Pocket 2 is an indication of comparable summer warmth to northern England today. Holman's (1993c) account of the Devensian (meaning all time after the Ipswichian and before the Holocene)

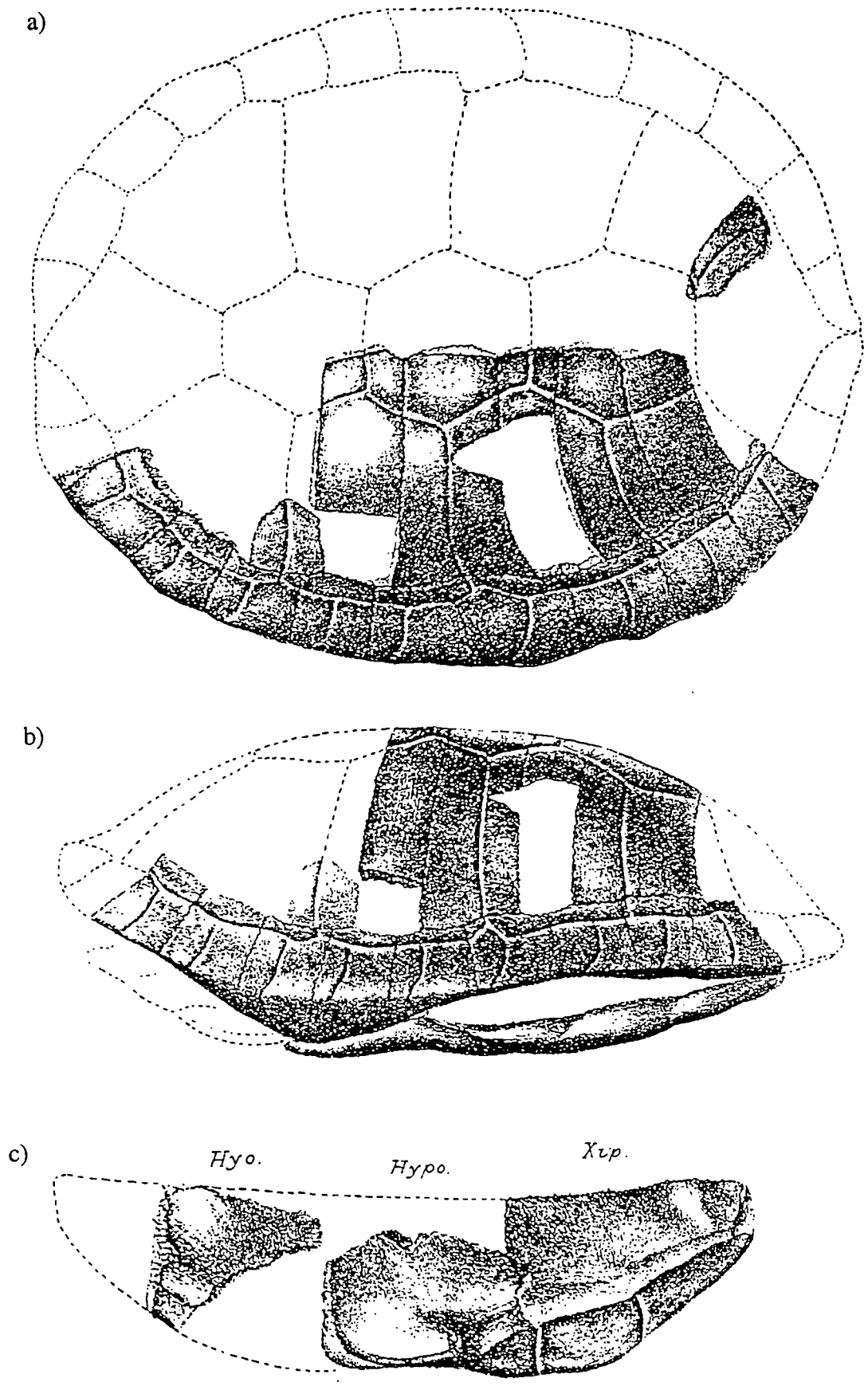


Figure 3.10:Remains of *E. orbicularis* from the 'Mundesley River Bed' (NCM collection): a) partial carapace (dorsal view); b) partial carapace and plastron (left lateral view); c) partial plastron (dorsal view) (after E.T. Newton, 1879; no scale given).

is simplistic and inaccurate, making no mention of temperatre episodes within this period. He suggested that *N. natrix* is cold-tolerant and, as it is recorded from within the Devensian cold stage gravels at Shropham, must have lived under periglacial conditions. *N. natrix* is a relatively thermophilous species, reaching the Scottish Borders in Britain today, and Shropham 'Pocket 2' was clearly deposited during interstadial conditions. The temporal definition of the Devensian timespan is a matter for debate. Authors such as Currant and Jacobi (1997) refer to temperate episodes after the Ipswichian *sensu stricto* as being part of the Last Interglacial *sensu lato*. Until formal agreement is reached, it might be more appropriate to refer to interstadial deposits such as Shropham Pocket 2 as belonging to 'later Stage 5' rather than using a generic term such as Last Interglacial or Devensian.

Levaton Cave, near Newton Abbot in Devon, contains a fissure filling, with amphibian remains identified only as *Rana* sp. and *Bufo* sp. found in a basal layer (Carreck, 1957). The associated small mammal fauna suggested an Early Devensian age, comparable with that of much of the Ightham fissure deposits described by Newton (1894). Holman (1985) believed the herpetofaunal remains from Ightham to be of Holocene age, however, and the Levaton amphibians are probably not synchronous.

Stuart (1982) noted several records (also listed by Holman, 1990; 1993c), of mainly indeterminate anurans, from Devensian sites as follows: Coston, Norfolk: *Rana* sp. or *Bufo* sp.; Upton Warren, Worcestershire: *R. temporaria*; Wilmen's Pit, Middlesex: 'amphibians'. It would seem that these sites represent Stage 5 and Devensian interstadials. However, where only *R. temporaria* and *L. vivipara* are present, without other lines of evidence, no climatic inferences can be made. Both species have Holarctic distributions today, and may have been present in premafrost free areas of Britain during Devensian cold-stages. The *N. natrix* bones from Shropham Pocket 2 (Holman, 1992e) provide the most certain herpetological evidence of a post-Ipswichian temperate phase within Stage 5.

3.5 Devensian Lateglacial and Holocene

From the current study, it appears that sites of Devensian Lateglacial and Holocene age, with herpetofaunal remains, are very widespread. However, only a few have been published, though numerous Late Holocene records of 'frog or toad' are contained within archaeological literature. It has not been possible to search out most of these undeterminate records during this project.

Only one herpetofauna of unequivocal Lateglacial age has previously been published. Alluvial channel-fill deposits of Late Pleistocene age are widespread in the Lea Valley, southwest Essex, and one such channel, of Lateglacial age, was shown to contain an abundant small vertebrate assemblage (Allison *et al*, 1952). M. Smith tentatively identified numerous anuran bones as *R. temporaria* and *B. bufo* (Allison *et al*, 1952), though it is unclear if other species were considered as possibilities. Hinton (1952) also recognised cranial elements of a small lizard, which he tentatively assigned to *L. vivipara*.

A herpetofauna from Ightham, Kent, is probably of early Holocene age (Holman, 1985). E. T. Newton first described fully the impressive vertebrate fauna from the site in the Lower Greensand's 'Kentish Rag', which is fissured at many locations in Kent and is often filled with bone-rich brick-earth (Newton, 1894). The column of sediment in the Ightham Fissures probably spans much of the Devensian, and its vertebrate fauna includes *Mammuthus primigenius, R. tarandus, Hyaena* and *E. caballus* (Newton, 1894). The herpetofaunal remains described by Newton were not fully identified, but Holman (1985; 1989b) provided a comprehensive list: *T. helveticus, B. bufo, B. calamita, R. temporaria, A. fragilis, N. natrix, C. austriaca* and *V. berus.* The record of *B. calamita* is of great interest as the species is no longer present in Kent, though it was fairly widespread in other parts of southeast England until relatively recently (Taylor, 1948; Beebee, 1978). Also, *C. austriaca* has its only Holocene fossil record at Ightham. Many of the remains were preserved as partly or even fully articulated individuals, in particular those of *Triturus* and *A. fragilis.* The remains of the latter included one individual replete with its covering of osteoderms. Holman (1985) suggested that the herpetofaunal remains probably date to the early Holocene around 9,500 BP, with a climate at least as warm then as it is today. The exact stratigraphic position of the remains is not known, and no dating has been applied to the deposits. It is therefore possible that the herpetofauna might be of Lateglacial or composite age. Radiocarbon assays would be very useful, particularly as this herpetofauna has important palaeozoogeographical implications. In the light of recent studies, bufonid material from the Ightham fissure has been re-examined by the current author and is discussed in a later section. Holman's (1985) identifications are supported.

Holman (1988) described a rich assemblage of herpetofaunal remains from Cow Cave, near Chudleigh in Devon. Its age is uncertain, and was interpreted as Lateglacial, early Holocene or both (Holman, 1988). The mammalian assemblage is mixed, and comes from a variety of sediments, possibly dating back to the Early Devensian (R. Jacobi, pers. comm., 1997). Three amphibians and two reptiles were identified from Units I, II and IV: *B. bufo, B. calamita, R. temporaria, A. fragilis* and *V. berus.* Again, the record of *B. calamita* is notable as the species is not present today in southwest England. The bufonid material from Cow Cave has been re-examined by the current author and is discussed in a later section. The identifications were supported in most cases, though some individual elements labelled as *B. calamita* were re-assigned to *B. bufo.*

The Whitemoor Channel, near Bosley in East Cheshire, yielded amphibian remains from a layer of *Chara* marl in a small Holocene lacustrine basin, filling a depression cut by a glacial meltwater channel. Johnson *et al* (1970) described the molluscan and ostracod assemblages from the marl, and the floral history of the marl and overlying peats. The marl was correlated by comparison with the chronostratigraphy at Red Moss (Lancashire) to pollen zone V, between c.7,200-8,000 BP. The amphibians are as follows: *T. vulgaris, T. helveticus, Triturus* sp., *B. bufo, B. calamita, Bufo* sp., *R. temporaria* and *Rana* sp. With the exception of *B. calamita*, this

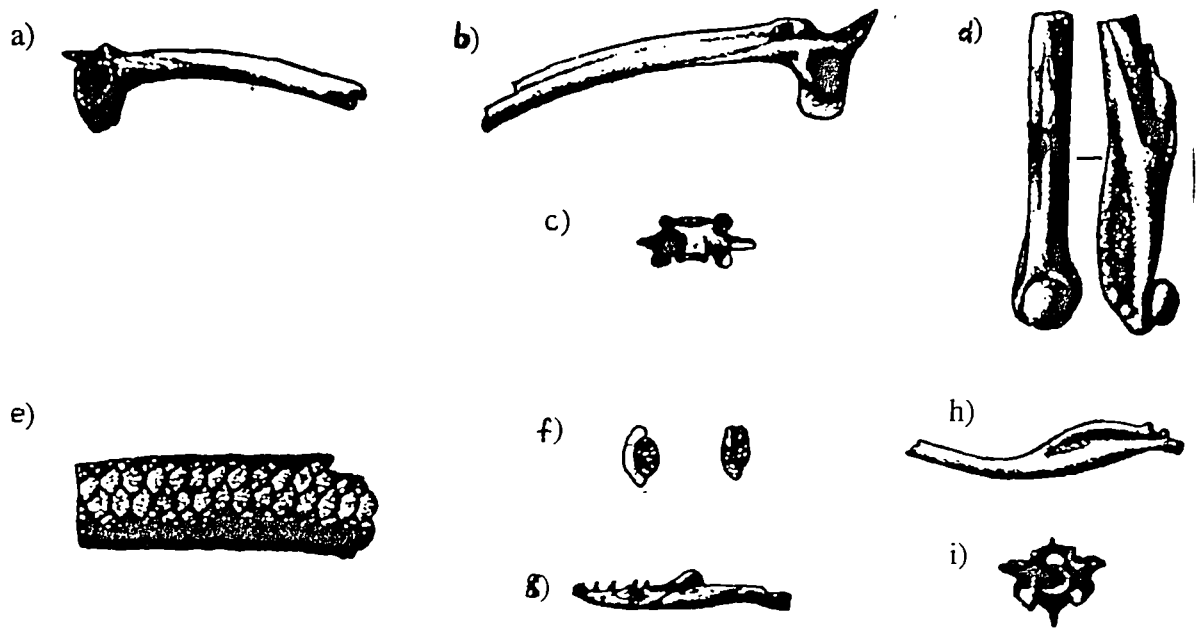


Figure 3.11 : Herpetofaunal remains from Ightham (BM(NH) collection): a) R. ilium of '*B. bufo*' (*B. calamita*); b) left ilium of *R. temporaria*; c) trunk vertebra of *R. temporaria*; d) right humerus of male *R. temporaria*; e) intact body section of *A. fragilis*, with osteoderms attached; f) two osteoderms of *A. fragilis*; g) left mandible of *A. fragilis*; h) left mandible of *V. berus*; i) trunk vertebra of *V. berus* (after E.T. Newton, 1894).

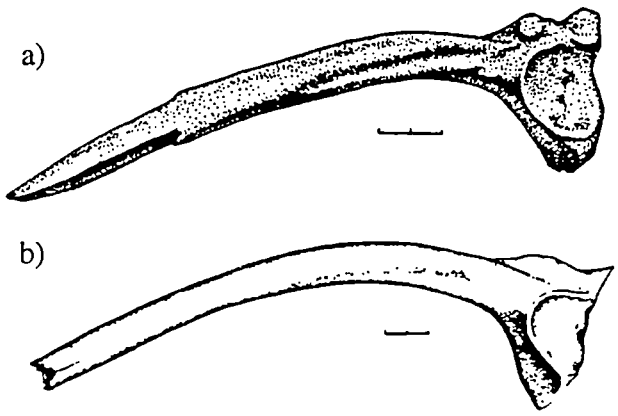


Figure 3.12: Left ilia of *B. bufo* from Whitemoor Channel (Cheshire) in left lateral view: a) NCM 143.949 (97), identified as '*B. calamita*' by Holman and Stuart (1991); b) NCM 143.949 (104) (after Holman and Stuart, 1991).

fauna could be found in the area today. Re-examination of the material has shown that the identification of *B. calamita* is incorrect (see Chapter 6).

The Creag nan Uamh Caves in the Assynt district of Sutherland, northwest Scotland have yielded a rich assemblage of vertebrate remains dating from the Middle and Late Devensian and Holocene periods (Peach and Horne, 1917; Callander *et al*, 1927; Lawson, 1981; 1995). Newton (1917) identified remains from the red 'cave-earth' which he assigned to *B. bufo, R. temporaria* and '...with hesitation...' to *B. calamita.* In the light of recent studies of numerous remains by the current author, it is concluded that the latter was a misidentification (see Chapter 6). It was based on a small humerus and other unspecified elements, besides which *B. calamita* would be very unlikely at such a northerly location during the Holocene. New material from the caves is discussed in detailed in a Chapter 6, and radiocarbon ages obtained are discussed.

Remains of *E. orbicularis* were recorded from East Wretham, Norfolk, during the last century. Newton (1862) identified remains but did not describe them systematically. The substantial portions of carapacial and plastral remains are now known to belong to three individuals (Stuart, 1979). These are the most complete remains of *E. orbicularis* known from the British Isles. Isberg (1929) and Degerbøl and Krog (1951) have described numerous complete shells and partially articulated skeletons of *E. orbicularis* from Holocene deposits in Sweden and Denmark repectively, so such finds are not unique. The East Wretham *Emys* remains must have lived under a mean July temperature of at least 1-2°C higher than today, during the Holocene climatic optimum (Stuart, 1979). The associated deposits appear (palynologically) to date to chronozone Fl II (pollen zone VIIa of Godwin, 1940) (Hall, 1979).

Holman (1987b; 1991) identified *B. bufo, R. temporaria* and *N. natrix* from Happaway Cave, Torquay, Devon, and a single *N. natrix* vertebra from Dog Holes, Warton, Lancashire. He suggested that neither of the sites may have been particularly old, though it seems this was based only on the appearance of the bones. It is assumed that they may date to some time during the Holocene. Further records of *R. temporaria* from Netteswell (Essex) and *B. bufo* and *R. temporaria* from Bathford (Somerset) were listed by Holman (1987b). Their ages are unknown, as the bones are housed in the anuran collections of the Natural History Museum (London) without geological information, but they are most likely to be Holocene.

Only a small number of archaeological records are included here, though many others have been made. A Megalithic tomb site, Barclodiad y Gawres on Anglesey, was excavated during 1952 and 1953 (Powell and Daniel, 1956) and produced some small vertebrate remains. Pumphrey (1956) identified several amphibian and reptile species (the vernacular names given have been replaced here by scientific names): *Rana* sp., *B. bufo, B. calamita, N. natrix.* A Holocene record of *B. calamita* from this part of the British Isles is intriguing. Unfortunately the material cannot be traced today. The imaginative taphonomic interpretation given by Pumphrey for such an accumulation of frog, toad and snake bones is equally intriguing. Nevertheless, the remnants of a witch's ceremonial 'special stew' cannot be supported by any scientific evidence.

A Megalithic cemetery at Carrowmore, c.8km west of the City of Sligo, is notable as it produced the first fossil record of *B. calamita* from Ireland. Ove and Persson (1980) recorded several partly articulated skeletons of *B. calamita* during the excavation of graves. The contextual information (Burenhult, 1980) is sparse, and the age of the bones is unclear. It has been suggested that the remains may even be recent (Ove and Persson, 1980). *B. calamita* in Ireland has never been recorded outside Kerry, and there are important zoogeographical implications, especially as it has been suggested that *B. calamita* may have been introduced to Ireland recently (see Beebee, 1984). Samples of bone are currently awaiting radiocarbon age determination (L. Keane, pers. comm., 1997). Scharff *et al* (1902) recorded 'frog' from throughout apparently Holocene (and perhaps Devensian) sediments in Plunkett Cave, Keishcorran, Co. Sligo. This site is has been re -examined and is discussed in Chapter 6.

Rana sp. and Lacertidae indet. were recorded from Steetley Cave, Creswell (Derbyshire), in association with Mesolithic archaeology and woodland pollen spectra (Bramwell *et al*, 1984). Sediments from a well at the Tiddington Roman settlement, near Stratford-upon-Avon in Warwickshire, were examined by Holman (1992c). The remains of *T. vulgaris* or *helveticus, B. bufo* and *R. temporaria* amounted to hundreds of bones which had accumulated since the well was dug around 200 AD (Holman, 1992c). Raxworthy *et al* (1990) carried out a detailed study of anuran remains from the Repton (Derbyshire) archaeological site, spanning from 700-1600 AD: *R. temporaria* and *B. bufo* were found in abundance. Interestingly, almost all of the *B. bufo* bones are from deposits laid down after 1300 AD. Various other archaeological excavations in southern England have commonly involved anuran or 'amphibian' remains (D. Sergeantson, pers. comm., 1995), but specific identifications are mostly lacking. Certainly, a large quantity of Holocene herpetofaunal data could be expected to accrue from archaeological collections.

4 Methodologies

4.1 Existing comparative material studied

Various institutions likely to hold relevant skeletal material in existing collections were contacted, with the aim of borrowing or studying specimens. It soon became apparent that, on the whole, very little useful material is available in British collections.

The Department of Zoology at the Natural History Museum (London) holds a variety of amphibian and reptile skeletons, but these are generally articulated and in poor condition, dating from the nineteenth century. Skeletons of green frog species, and *Bombina* have been studied, but these could not be borrowed, and the articulated nature of material meant that their usefulness for comparative studies was limited. The Oxford University Museum had no European ranid skeletons when a request was made (J. Pickering, pers. comm.). Cambridge University Museum has no records of frog material. The Institute of Archaeology, University College London, hold a number of skeletons of *R. temporaria* for teaching purposes, three of which have been loaned. Southampton University's Faunal Remains Unit hold a few British amphibian and reptile species. These could be studied on the premises, and often consisted only of partial specimens.

A full search of all British zoological, palaeontological and archaeological collections would have been too time-consuming, thus it was decided that a new reference collection had to be gathered. It is abundantly clear that there is a general lack of amphibian and reptile skeletal reference material in British Museums and University collections, reflecting the corresponding lack of expertise in this field.

Some continental collections are much more comprehensive, but there are obvious limitations in relying long-term on borrowed material from other countries. A visit to the Polish Academy of Sciences in Kraków proved very worthwhile. Z. Szyndlar kindly accommodated the author for two weeks in April 1995. Recent specimens in the personal collection of Z. Szyndlar (ZZsid) and numerous fossil remains from important Polish localities were studied. The collections of the Museo Nacional de Ciencias Naturales in Madrid include a large number of comparative skeletons. Unfortunately, the author was not aware of this until much of the thesis had been written. Nevertheless, through the kind cooperation of B. Sanchiz, a recent visit allowed the study of species not collected during the project. The Nationaal Natuurhistorisch Museum in Leiden, Netherlands, has only one useful skeleton of '*Rana esculenta*'(M. Hoogmoed, pers. comm.). No reply has been received from Drs. R. Günther and G. Böhme, at the Museum für Naturkunde in Berlin, Germany. The Museum Koenig in Bonn, Germany, have no useful skeletons of green frogs, for which a request was made (W. Böhme, pers. comm.). No reply was received from J.C. Rage, at the Laboratory of Vertebrate and Human Palaeontology, University of Paris, France.

4.2 Laboratory preparation of comparative material

A great deal of time has been spent during the course of this project, carrying out laboratory preparation of comparative specimens. Corpses were donated by various people, and collected in the field by the author. Preparation of disarticulated comparative skeletons, from these corpses, has been a time-consuming part of the project, requiring careful dissection and processing. A variety of techniques for preparing skeletons have been described in the literature (Mahoney, 1969; Davis and Payne, 1992; Legge, 1993). Not all of these have been tried, but some clearly work better than others.

TECHNIQUES EMPLOYED

Several preparation techniques have been used, with very variable success, involving maceration in a heated enzyme solution. The quality of recovery has been found to be dependent not only on the size, state of decay and type of animal being prepared, but also on the reagents, temperature, time elapsed and care employed in the process. It is preferable that a specimen has not been preserved in alcohol as this chemically alters the soft tissues, so that a more complex process is needed in order to digest them. The overall process of preparation is lengthened, requiring extra reagants, and is less likely to produce satisfactory end products. Desiccated and partially-decayed specimens are easier the prepare, as less tissue has to be removed. Freezing of specimens is acceptable, and may weaken soft tissues favourably.

The most effective process, and that which has been used most extensively, is that of simple enzymic maceration, as described by Mahoney (1969). Initially, trypsin was used (from pig pancreas), and was effective, but this was replaced by the vegetable enzyme papaine (from papayas). Trial and error was employed, with solutions of between 1-2%. Temperatures, preparation times and water solution volumes were varied, until a set of optimum conditions were found. Enzymic maceration was found to be most effective with 1.3% papaine (by mass), in aqueous solution, maintained at 38^{o}C in a thermostatically-controlled electric waterbath. Preparation took 24-48 hours, depending on the size of the animal and the degree of defleshing.

Relatively fresh specimens could be skinned, gutted and defleshed fairly easily; frozen specimens were defrosted in hot water first. Skinning of anurans is easiest, due to the relatively large size of their limbs and digits. They can be skinned by making an incision along the belly, and removing the viscera. By making incisions to the upper arms and thighs, the skin of the four limbs is easily removed, inside out, right to the ends of the toes. The torso and head are skinned in the same way, but the skin of the throat is best left intact, in order to prevent loss of hyoidal bones. Some skin tends to be left around the jaws, but this does not affect the defleshing process. The limb muscles are attached only by tendons at the ends of the long bones, and are easily removed by careful use of a scalpel. Total defleshing is not necessary; evisceration and removal of most of the limb muscles is sufficient. Snakes can be skinned fairly easily by making a long incision along the ventral surface. The viscera fill a long cavity and are easily removed, after which the skin can be

peeled off, though the head and tail tip may be difficult to skin. Only ribs, vertebrae and a minimum of soft tissue are left: no defleshing is needed, and maceration is swift. Slow-worms are smaller and more difficult to skin. The skin is rigid, due to its content of bony osteoderms, and must be peeled off with care and prepared with the rest of the skeleton to retrieve the osteoderms. Newts are difficult to skin completely, though this is not necessary as a partial covering of skin does not seem to hamper the maceration process. The thin skin rips easily, and attempting to skin the limbs may result in the loss of digits. Newts can be eviscerated, but no defleshing is needed. The minute bones are remarkably resilient to the action of the enzymes, and a minute, intricately sculpted skeleton is produced. Lizard skin is fairly tough and, despite the small size of their limbs, the skin can be removed inside out. A ventral incision should be extended to the limbs and around the shoulders and waist. Other than evisceration, the minimum of defleshing is necessary.

Elongate animals such as snakes, once gutted and skinned, had very little tissue left on them and were completely disarticulated after 24 hours. Decaying specimens, too unpleasant to dissect, had to be prepared whole, and generally took longer to disarticulate. Regular inspection was essential. Some body parts (e.g. heads) take longer than the rest of the skeleton to prepare. If a specimen is left too long, in order to fully disarticulate the head, then other elements, such as long bones, may become badly corroded and fragile.

Each specimen was prepared separately, in glass beakers containing around 500-750cm^3 enzyme solution: as a rule, about ten times the volume of the animal being prepared. A fume-extraction cabinet was used for the operation, due to the unsavoury nature of the fumes emitted, and their potentially biohazardous nature. Once maceration was apparently complete, the liquid waste was decanted off from each beaker, in a well-ventilated area. The disarticulated residue was then rinsed several times in the beaker, and the waste water decanted through a fine-meshed (250μm) sieve to prevent the loss of smaller bones. Upon drying, the bones were normally clean and whitish in colour. Occasionally, an odour persisted due to incomplete removal of internal bone tissues, and some skeletons (notably freeze-dried specimens) remained very greasy. To address this problem, some specimens have since been treated by soaking in approximately 1:8 aqueous solution of hydrogen peroxide, for several hours. This was successful in degreasing, deodorising and bleaching the skeletons, but can cause damaging corrosion if left too long. Rinsing with acetone was effective at degreasing bones also, and addition of detergent to a maceration solution is also helpful.

After final rinsing, skeletons were air-dried at room temperature, and archived in partitioned plastic trays for ease of study. Cranial elements were separated from vertebrae, and tetrapod appendicular elements were appropriately separated where possible. Initially, several specimens were prepared with a single forelimb and a single hindlimb in separate beakers, in order to identify and establish the body position of appendicular elements.

Other less successful preparation techniques were attempted. Detergents and enzyme-based washing powders, in aqueous solution, had been suggested as a useful technique, but proved too

ineffective and slow to be useful, except perhaps for very small animals. Specimens preserved in alcohol (100% IMS or 25% opresol/75% IMS is often the case) required much more preparation. Skinning and defleshing was not as easy, as preserved tissue is somewhat rubber-like. Alcohol-preserved specimens also required a more prolonged treatment. This involved maceration in a solution of 2% pancreatin (from beef pancreas), with 1% sodium sulphide in saline solution. The solution had to be maintained at around 50°C, but preparation took much longer than for fresh specimens (at least two weeks), and was not always effective. Addition of a strong detergent was apparently helpful. Only a handful of specimens were prepared in this way, and success was strongly controlled by their size, preservation media and history. Some specimens were not completely prepared even after eight weeks, and it was concluded that defleshing of alcohol-preserved specimens was too inefficient to be time-effective. Bones were still undamaged after this time, but it appeared that the soft tissues varied in quality between specimens, probably in relation to the time spent in alcohol.

During the latest stages of the project, some changes to the papaine method preparation were . Several large specimens were immersed in a 5% aqeous solution of potassium hydroxide for several days, at room temperature. As this failed to do any more than perhaps soften the skin and flesh of the specimens, the solution was drained off and normal papaine treatment was applied. This produced remarkably efficient results. Within 24 hours, perfectly prepared skeletons were achieved, probably due in part to the preliminary action of the potassium hydroxide.

OBSERVATIONS AND PROBLEMS

As the process was refined, it became necessary to exercise a great deal of care over the time allowed for preparation. As it is difficult to accurately estimate the volume of flesh to be dissolved, the volume of reagant may be insufficient or excessive to requirements. An insufficient volume will mean that the process takes longer, or that unsatisfactory defleshing and cleaning of the bones occurs. Excessive enzyme solution will speed up the defleshing process so that the process has to be regularly inspected. More problematic is the unequal effect that excessive reagant has on the defleshing of different parts of a corpse. It is difficult to skin a corpse totally, particularly ones which are already undergoing decay. Sometimes defleshing appears to be complete, as disarticulated bones are visible in the beaker, but upon decanting and straining it is obvious that some body parts are incompletely defleshed. This tends to be a problem with the head, manus and pes, particularly of newts and lizards, especially where skinning has not been completely carried out. Skin often acts as an effective barrier to the enzyme solution, often only removing pigment. The long bones and vertebrae can be beautifully cleaned and disarticulated, whilst leaving an intact lizard head or foot. It appears that the relatively different resistences of soft flesh and sinews must also play a part. A skeleton can have been totally defleshed, but certain limb joints have remained loosely attached by tendons. Overall, a weaker solution given longer to prepare a skeleton, is safer than a more potent, faster preparation. The chemistry of the reaction must be that it occurs at a rate

which is closely related to the temperature and concentration of the enzyme, within a very narrow band. Outside this, the reaction's efficiency drops sharply.

A useful method of keeping the vertebral column in the correct order is the insertion of a length of nylon filament (such as fishing line) at the dissection stage. After skinning and evisceration, the head should be separated from the neck so that a length of nylon line can be inserted into the neural cavity of the exposed vertebra. This can be pushed easily along the vertebral column with minimal force and guidance. It becomes more difficult as the neural cavity decreases in size, but most of the vertebral column of caudate species can still be penetrated. For anurans, the neural canal is large and complete penetration is a simple procedure. The free ends of the filament can be tied together in order to keep the vertebrae in sequence whilst all soft tissues are digested during maceration.

The most severe problem experienced in the preparation of skeletons has been when the time allotted for maceration was overestimated. If maceration was left too long, the enzyme weakend and dissolved bones quite severely. This caused total loss of the skeleton in some cases, but more often reduced the ends of long bones, and caused exfoliation. Weaker bones were more severely damaged and the whole process was worsened by the inequality of flesh thickness at various parts of the body. Even after skinning and defleshing, some parts of the skeleton are almost exposed already, whereas other parts are surrounded by flesh. This is not a problem with weaker solutions, even after considerable amounts of time.

Tissue samples were taken from the green frogs (*R. ridibunda* and *R. esculenta*) provided by English Nature, before their preparation. The gut of each specimen was retained and preserved in 100% alcohol, individually labelled, for future dietary studies. A further tissue sample (at least $1cm^3$ of internal organs and/or leg muscle) was also removed from each frog, labelled, and frozen for future study. Toes from some specimens were clipped and immersed in 100% IMS, for future DNA studies, but all other soft tissues were discarded.

One several occasions, the stomach contents of specimens were recovered from the skeletal residue, identifiable as the animals' last meals. Partly digested skeletal remains from the stomach of a *N. natrix* specimen (CGO 13/4) were identified as one *R. temporaria* and one *T. cristatus* (Gleed-Owen, 1994). Another *N. natrix* contained a juvenile *B. bufo*, and a small *Triturus* sp. A polecat (*Mustela putorius*), was also found to contain a *T. cristatus* and a juvenile *R. temporaria*, demonstrating it to be one of the predators of these species (Gleed-Owen, 1996). Specimens of *L. vivipara* (CGO 41/1) and *L. agilis* (CGO 18/1) contained various unidentified insects, including a sand wasp (Order: Hymenoptera). One *B. calamita* specimen (reference number not recorded) contained three large black diving beetles, and one *T. vulgaris* (CGO 7/5) contained a pair of valves of *Pisidium nitidum*.

4.3 Study methods

Throughout the course of gathering a comparative collection, a number of methods have been employed to study and record the osteological character of each species in as much detail as possible. Familiarisation with individual elements within the skeleton and between families was achieved first, by comparison with literature drawings and descriptions. Comparative study between species was possible as the material became available and as proficiency increased. Recording has been primarily descriptive, but drawing, optical photography and scanning electron microscope (SEM) photography have all been employed. Morphometric measurement of such small bones is difficult and has been found to be of limited use in this field (Szyndlar, 1984). Visual comparison of morphology is both more effective and reliable than measurement, as well as more enjoyable. This is especially true for most amphibian and reptile species, as they are often recognised by subtle micromorphological differences in bones which, overall, have very similar shapes and sizes.

OPTICAL MICROSCOPY

Light microscopy, using low-power binocular microscopes, has been sufficient for most examination and allows the manipulation of individual bones required for detailed visual analysis. A Kyowa SDZ-PL (x7 - x45) was used for most of the work, but also a Zenith MBS10. A Leica microscope, fitted with a camera lucida, was also used on occasions. Comparative specimens and fossil material has been studied using optical microscopy with reflected light, which allows easy manipulation of bones, direct comparison of specimens at low magnification and visual familiarisation of morphology. The isolation of identification criteria from modern specimens has been attempted wherever possible, so that this information can be applied to fossil material. The resultant osteological descriptions are discussed in Chapter 6.

SCANNING ELECTRON MICROSCOPY

The preferred method of recording smaller bones has been by using SEM micrographs. The level of detail achieved is superior to that which is possible by optical microscopy, and allows ready comparison of micrographs. Diffusion and refraction of light, which can be problematic under light microscopy, is removed. A clearer image is presented, showing fine details of microtopography, shadow, grain and texture. The process is relatively fast and careful selection of useful elements for SEM provides an invaluable visual key for easy comparison of bones. Small adhesive carbon-coated labels were applied to aluminium stubs (12mm and 25mm diameter). A single bone was placed in the centre of each labelled stub, and submitted for SEM photography. Each stub and bone was vacuum-coated with gold and placed in the SEM. Electron micrography was carried out at magnifications between x20 and x40, on a camera attached to the electron microscope probe (C. Lovering, pers. comm.). The results from elements of modern specimens are shown in many of the figures given in Chapter 5. A large number of the fossil remains studied have also been SEM

micrographed, and various figures are shown throughout Chapter 6. A black and white, millimetre scale bar is printed automatically on each photograph, except at the lowest magnifications where a single white centimetre bar is shown (such cases are indicated in the captions). Elements with dimensions greater than about 10mm cannot be photographed by SEM, unless composite images are taken.

DRAWING

Bones which are either too large for SEM photography (i.e. greater than c.10mm), those belonging to collections which cannot be gold-coated, or specimens which are to be radiocarbon dated, have in many cases been recorded by detailed illustration using pencil or ink. A camera lucida attachment on a Leica binocular microscope was used for most drawings. The same technique was also applied during periods of residence at the NHM, PAS and MNCN. The level of accuracy and detail achieved by SEM photography cannot be matched, but drawing can give a better representation of relief and overall shape.

5 A manual for the identification of fossil herpetofaunal remains

5.1 Introduction

This chapter is a preliminary attempt at providing a descriptive key for the identification of herpetofaunal remains. It is incomplete, because for some species, the comprehensive study of sufficient specimens required to achieve certainty in diagnosis was not possible, within the timescale of the current project. The illustrations and SEM micrographs are to be used in conjunction with the descriptive keys. It is hoped that this work can provide the basis for future palaeoherpetological training.

As a group, European amphibians and reptiles have still received much less attention from palaeontologists, than many other animal groups. Within the group, there are inequalities in the volume of descriptive and palaeontological work carried out for each of the herpetofaunal tribes. For example, more is known about the identification of frogs, toads and snakes than newts or lizards. Thus, newts and lizards cannot often be identified specifically. This has also created an inevitable inconsistency in the way fossil material has been dealt with, and probably reflects both the differences in interests of workers and the complexities of studying certain groups. Studying the osteology of amphibians and reptiles, in order to identify individual elements from fossil assemblages, is considerably more difficult than other groups such as mammals, molluscs and beetles. The remains of amphibians and reptiles fall within the size range termed as microvertebrates and are correspondingly less easily recognised than large mammals. In contrast with small mammals, the teeth of amphibians and reptiles are much less diagnostic and generally too small to be retrieved by normal sieving methods. Neither is identification possible on the basis of one skeletal element which is consistently diagnostic across species, genera and families. Molluscan evidence involves recognition of the shape of only one or two shells for each species. Palynology involves the recognition of one consistent pollen grain morphology for each species. Almost all small mammals are identified using tooth morphology. The diagnosis of herpetofaunal remains is less simple and requires the consideration of the whole skeleton. As this would involve a working knowledge of around 200 skeletal elements for each of the 37 species considered here, a certain amount of discretion is required. On the other hand, in order to maximise the usefulness of the generally fragmentary herpetofuanal assemblages which become available, an ability to identify species from as many different skeletal elements as possible would be of obvious benefit.

The most detailed studies on the biology of amphibians and reptiles in Europe were carried out in the latter part of the 19th century, and the encyclopaedic nature of these early works has not been matched. A general grounding in the nature of skeletal morphology and variation has been aided by use of a number of monographs. Those which deal with general skeletal description for the amphibians and reptiles include Zittel (1887-90), Ecker (1889), Gaupp (1896), Boulenger

(1897-8), Romer (1956; 1966). Most of these osteological descriptions and zoological texts are written in English or German, and have excellent illustrations. In contrast, most of the subsequent palaeontological work has been published in a number of other languages, including German, French, Spanish, Polish, Russian, Czech and Serbo-Croat. There has been a distinct change from pure anatomical description, as was the case during the latter part of the nineteenth century and the early twentieth century, towards applied palaeontology and other interrelated disciplines. The nature of descriptions in this literature is inconsistent and fragmentary, though collectively it is very useful. In the absence of comprehensive descriptions in any one text, authors regular cross-reference each other. Comprehensive osteological descriptions, for use in palaeoherpetology, are conspicuously overdue for this group of animals. There is almost no existing British literature on palaeoherpetological identification, and the continental literature is widely scattered. There are no identification keys for any of the amphibian and reptile groups studied, and no group has been comprehensively described.

Previous identification of British herpetofaunal material (e.g. Holman *et al,* 1988; 1990) has mostly relied upon one or two skeletal elements, usually the ilium. The ilium is undoubtedly one of the most useful elements in diagnosis, but there are other commonly-preserved elements with diagnostic value. By continuous referral to the drawings given by Böhme (1977), it appears that Holman has not consulted type material in most identifications. Whilst this is probably safe for some species, and for the few elements illustrated by Böhme (1977), much greater care is required in the identification of *Rana* species. Even with a range of comparative material at hand, the identification of *Rana* from ilia is difficult, and should not be attempted from drawings alone. Böhme (1977) and Böhme and Günther (1979) offered notes of caution over the identification of anurans from ilia, and could not distinguish between green frog ilia conclusively, and clearly did not intend the illustrations to be used as a definitive key. Despite this, Holman *et al* (1988; 1990) have specifically identified green frog ilia, giving the resulting impression that the text (in German) has not been consulted as much as the drawings. Also, the need for study of elements other than those figured by Böhme (1977), in order to maximise the fossil material available, has not been addressed sufficiently. Holman is still in possession of much of the material he has identified, and re-examination has not been possible. Those sites which have been re-examined by the current author are discussed in Chapter 6.

The osteological descriptions given in this chapter are the product of an in-depth study of the reference specimens studied for each species, combined with an overview of existing knowledge. The result is intended to be useful as a manual for future workers, and is correspondingly detailed where this has been necessary. The accumulated information provides an overview of existing knowledge, together with the results of the osteological studies of the current project. This is presented as an osteological account of the diagnostic criteria isolated for each species. An important part of the current study has also been the preparation of an SEM key for herpetofaunal remains. This is far from complete, but a large number of micrographs are presented in this

chapter. These have proved to be a very useful supplement to real type material, as they allow the viewing of bones in greater clarity than optical microscopy allows. It is hoped that this key will be of use to future workers, used in association with the accompanying descriptions.

It has not been possible to gather reference material for all the species considered, but in these cases as much information has been derived from existing literature as possible. Appendix 1 lists all comparative specimens prepared and studied. Ideally, a sample of twenty specimens for each species would be studied to assess intraspecific variation, but this has only been possible for *B. bufo*, *R. ridibunda* and *R. esculenta*. Nevertheless, specimens of twenty-four species have been collected, from the Salamandridae, Bufonidae, Hylidae, Ranidae, Emydidae, Lacertidae, Anguidae, Colubridae and Viperidae. No specimens have been collected for the Discoglossidae, Pelobatidae or Pelodytidae, but these gaps are filled by useful descriptions in continental literature. Nevertheless, it would be of obvious advantage that future efforts be made to collect specimens for the relevant species from these families. Fortunately, accounts by Böhme (1977), Boulenger (1897-8), Hodrová (1981), Sanchiz and Mlynarski (1979) and others (detailed in the respective sections which follow) show that these families are osteologically distinct and should not pose diagnostic problems should their remains be found. For the species with reference material available, efforts have been concentrated on more diagnostic elements, rather than being an exhaustive study of every skeletal element. This would be well beyond the bounds of a project of this size, and it is acknowledged that a certain amount of selectiveness has been exercised.

This section presents osteological descriptions for the skeletal elements studied, in as much detail as has been possible in the duration of the project. The identification criteria found to be diagnostic of species are outlined where possible. Greater detail is given to problematic areas and where previous literature has lacked sufficient detail for reliable identifications. Description cannot replace real comparative material, and it is emphasised throughout that the level of confidence required for firm identification cannot be achieved without reference material. The shape of a bone often gives a distinct overall character which often cannot easily be described by defining component character states, best summed up by the war-time expression 'G.I.S.S.' (general impression of shape and size). The logistics of this work have also set limits in some cases, and where study had not been exhaustive, this is made clear. The osteology of each group is addressed on a comparative basis, with discussion of characters which define genera and species. Drawings and SEM micrographs are incorporated and referred to in the text.

As osteological characters are relatively homogeneous within families, decription is given on the basis of individual families. The snakes (Ophidia) are dealt with together, though the species studied belong to two families, as their osteologies are very similar. Previous literature has often been confusing and inconsistent in its use of terminology, particularly for the anurans. For example, Sanchiz and Mlynarski (1979) used nomenclature derived from Bolkay (1919) and Vergnaud-Grazzini (1966). Hodrová (1981) used terms derived from Spinar (1972) and Gaupp (1896). Holman (1992) used Chantell (1964), and Böhme (1977) in his other publications.

Osteological terminology here is derived from a number of sources, and is intended to be clear and unambiguous. There are no irreconcilable differences in terminology employed in the literature, and in each case synonymy is easy to understand. Sources of terminology are acknowledged in each section, and where appropriate.

5.2 Salamandridae

(Salamandra salamandra, Triturus marmoratus, Triturus cristatus, Triturus alpestris, Triturus vulgaris, Triturus helveticus)

The European salamandrids have received very little attention in terms of osteology. To date no description or key has been published. Estes (1981) suggested that 'An extremely thorough quantitative comparative study of the skulls of Holocene *Triturus* is much needed...'; but this has yet to be accomplished. There is a fairly large volume of literature on Tertiary European fossil salamandrids (e.g. Herre, 1949; 1955; Sanchiz and Mlynarski, 1979; Hodrová, 1984; González and Sanchiz, 1986), but only some of this is relevant to the species studied here.

Francis (1934) gave a description of the skeleton of *S. salamandra*, but not in enough detail for it to be useful in palaeontology. W.K. Parker (1882) studied the skull of *Salamandra maculosa*, giving descriptions which are useful for comparison with *S. salamandra*. He also studied *Notophthalmus viridescens* and three other non-European salamandrids. The former is osteologically similar to *Triturus*, but no comparable studies have been carried out on the European species. Their skeleton has essentially the same form as the European salamanders, but differs in details such as a reduced frontosquamosal arch (Estes 1981). W.N. Parker (1897) briefly detailed the form of the urodelan skeleton, with illustrations of the skull of *Salamandra atra*.

The most useful study for palaeontological purposes to date is an unpublished paper by Szyndlar and Sanchíz, a copy of which was obtained from Z. Szyndlar. This study attempted to find phylogenetic links between *T. marmoratus, T. cristatus* and *T. vulgaris*, using osteological characters. The illustrations of vertebrae and cranial elements are good, and support the morphological characters of specimens in the current study. It has been noted that much of the skeletal morphology of *T. marmoratus* and *T. vulgaris* is very similar. The axial skeleton, as well as a number of cranial elements such as the exoccipital, are very comparable, and much more so than to *T. cristatus*. The contrasting external appearances and size difference of *T. marmoratus* and *T. vulgaris* masks skeletal similarities not formerly described. This suggests that re-investigation of phylogenetic relationships (beyond the scope of the current project), based on comparative skeletal morphology, may be fruitful. *T. vulgaris* and *T. marmoratus* have not previously been considered likely sister species.

Naylor (1978a) gave a detailed account of the systematic relationships of fossil and recent salamandrids, using features of the vertebral column. Among the taxa considered were three

species relevant here: *S. salamandra*, *T. alpestris* and *T. vulgaris*. Several simple illustrations of vertebrae were given, which make useful comparisons, but are not sufficient to be used as a key. González and Sanchiz (1986) and Scholz (1993) have also made detailed systematic studies of osteological and other characters, in attempting to define the phylogenetic relationships of *Triturus* and other salamandrids. Wake and Özeti (1969) dealt with the evolutionary relationships between the living genera, concluding that *Triturus* and *Salamandra* were fairly distantly related in phylogenetic terms. Rafinski and Pecio (1989) made a craniometric study of *Triturus* for discussion of the group's phylogeny. The data generated are not, however, useful for diagnostic purposes. González and Sanchiz (1986) used fossil evidence in their study of *Triturus* evolutionary relationships, but publications such as this lack descriptions which might be of use to palaeontology. Sanchiz (1988) has also discussed functional aspects of the vertebral articulation of the salamandrids.

Sanchiz and Mlynarski (1979) detailed Pliocene fossil salamandrids from Polish sites. The descriptions of fossil material are concise and clear, and the illustrations provide a useful comparison for the British reference specimens used in the current study. Their records included *S. salamandra* and *T. cristatus*, notable as the earliest occurrences of these species (Sanchiz and Mlynarski, 1979). Much of this material was studied during a visit to the Polish Academy of Sciences in Kraków, in 1995 (see drawings in Appendix 2). Late Pliocene salamandrids from the former Czechoslovakia were described by Hodrová (1984). This paper is of notable as it includes illustrations and descriptions of certain species on a comparative basis. The photographic plates of fossil *T. cristatus*, *T. marmoratus* and *Triturus* cf. *alpestris* appear similar, but perhaps not identical, to modern British specimens. The plates and illustrations of Pliocene *S. salamandra* trunk vertebrae show specimens which are decidedly narrower than the specimen studied here (CGO 11/1). This may demonstrate evolutionary change in the skeletal morphology of this species. Alternatively, narrower forms may still exist in living specimens today, but this could only be shown if the study of a range of modern specimens was possible.

There are no records of salamanders, and only a few records of newts from the British Quaternary. Specific identifications have often not been possible for some of these, as authors have found difficulty in differentiation (e.g. Holman and Stuart, 1991). It is also unsatisfactory for identifications to consider only the three native newts *T. cristatus, T. vulgaris* and *T. helveticus* as potential immigrants. Exotic anuran and reptile species have been found at British Quaternary locations, and such occurrences should be also be considered a likelihood for the urodeles.

A relatively small number of specimens have been studied here for each species, owing to difficulties in obtaining corpses. The descriptions below refer to the five newts of the genus *Triturus* considered in this study, and to *S. salamandra*. Osteological nomenclature follows that of Estes (1981).

CRANIAL BONES

The cranium consists of paired parietals, frontals, prefrontals, nasals, orbitosphenoids, maxillas, pterygoids, quadrates, squamosals, prootic-exoccipitals and vomers, with a single symmetrical parasphenoid. There are a pair of premaxillae in *S. salamandra,* but a single premaxilla in *Triturus.* The hyomandibular structure contains paired cornua, dentaries, mentomeckelians (consisting of articular/prearticular/splenial series). Very few cranial remains of salamandrids are found as fossils, and detailed study of many of these elements would probably not be worthwhile. The most robust and diagnostic elements are the 'dermal investing bones' (terminology of Duellman and Trueb, 1994), those which form the external surface of the cranium. Özeti (1967) provided good illustrations of individual cranial elements of *S. salamandra*; but the osteology of *Triturus* is not well illustrated in the literature.

Parasphenoid

The parasphenoid forms the floor to the braincase. It is very distinctive in its peripheral shape, apparently consistent within species, and is a very useful diagnostic element. It must be borne in mind that relatively few specimens have been studied, however, and that the potential for variation has not been investigated fully. The SEM microographs (Figures 5.2 and 5.3) are very useful keys for identification using this element.

The parasphenoid of *S.salamandra* is widely flared in its posterior region. It projects posterolaterally, with posterolaterally directed spines on each side, separated by a deep canal on the dorsal surface. These lobes connect with the prootic portions of the prootic-exoccipitals. Adult specimens should also be separable due to their larger size than *Triturus* specimens. The length of the parasphenoid in a *S. salamandra* specimen of 150mm total length was 11mm, as opposed to 8mm in a *T. cristatus* of 120mm total length. In *T. cristatus,* the posterior half is well-rounded but is constricted mid-length to its narrowest point. It is then flared slightly at the anterior end, with divergent lineae on the ventral surface. In *T. marmoratus*, the posterior region narrows slightly until beyond mid-length where it narrows more sharply into a tapering anterior portion.

The smaller newts (*T. alpestris, T. vulgaris* and *T. helveticus*) have typical parasphenoid lengths of around 4.5-5.5mm for specimens of 75-90mm total length, respectively. In *T. vulgaris,* the posterior half forms a rounded hexagon connecting anteriorly to a narrow projection with roughly parallel sides and only a third of the width of the posterior half. The anterior portion is always relatively narrow allowing distinction from *T. helveticus* which has its anterior portion is always relatively broad and slightly flared. The posterior portion in *T. helveticus* has a very angular sub-hexagonal outline and is widest at the two postero-lateral corners, which protrude posterolaterally as sharp lobes. There are an additional pair of small posterolaterally directed lateral spines, mid-way along the posterior region, best seen from the dorsal side (see Figure 5.2). Similar features are seen in *S. salamandra* and are allow distinction of *T. helveticus* from the well -rounded *T. vulgaris*. The edges of the posterior region in *T. helveticus* are concave and sharply

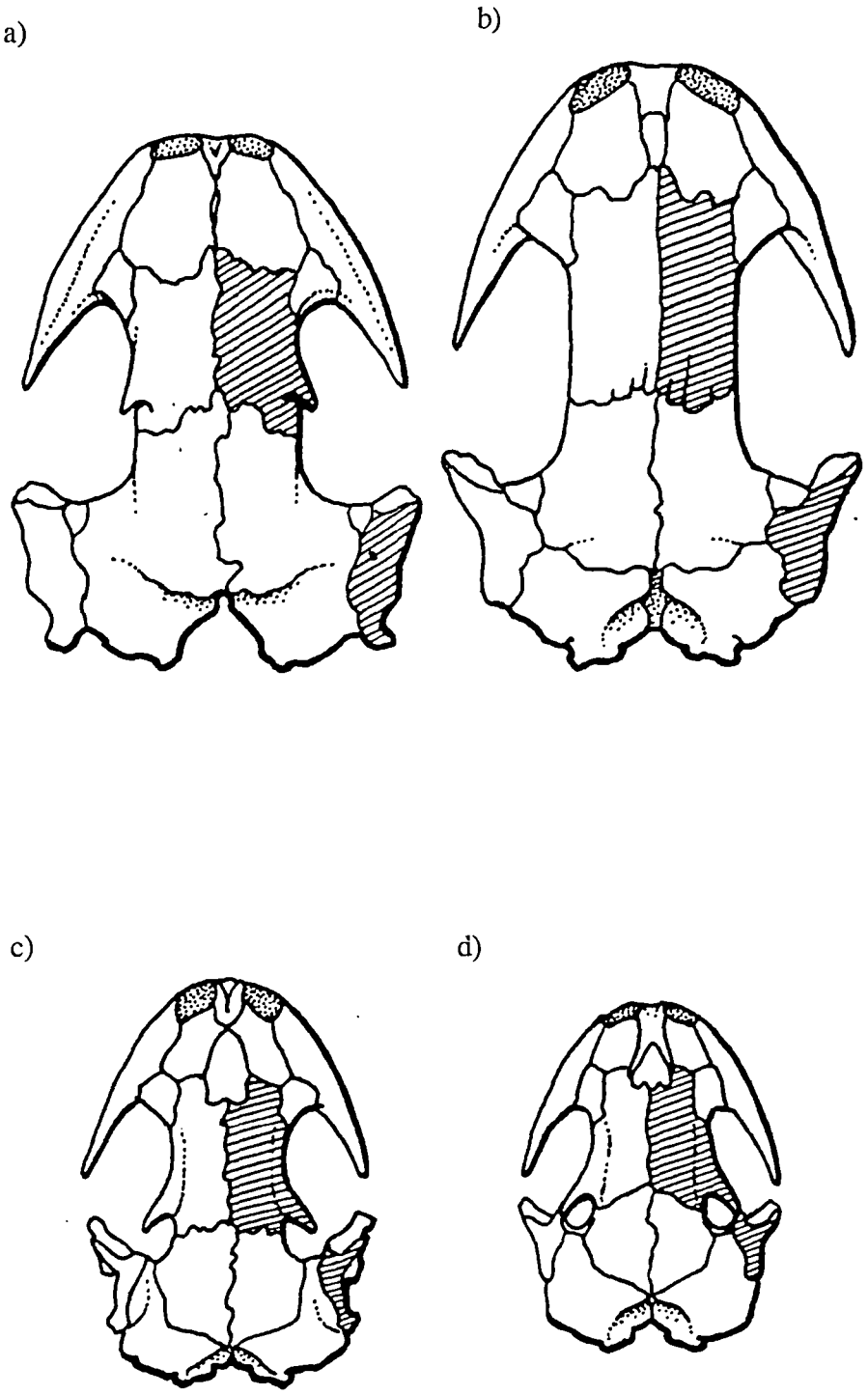


Figure 5. 1 : Cranium in dorsal view of: a) *T. marmoratus*; b) *T. cristatus*; c) *T. vulgaris*; d) *T. helveticus* (after Arnold and Burton, 1978).

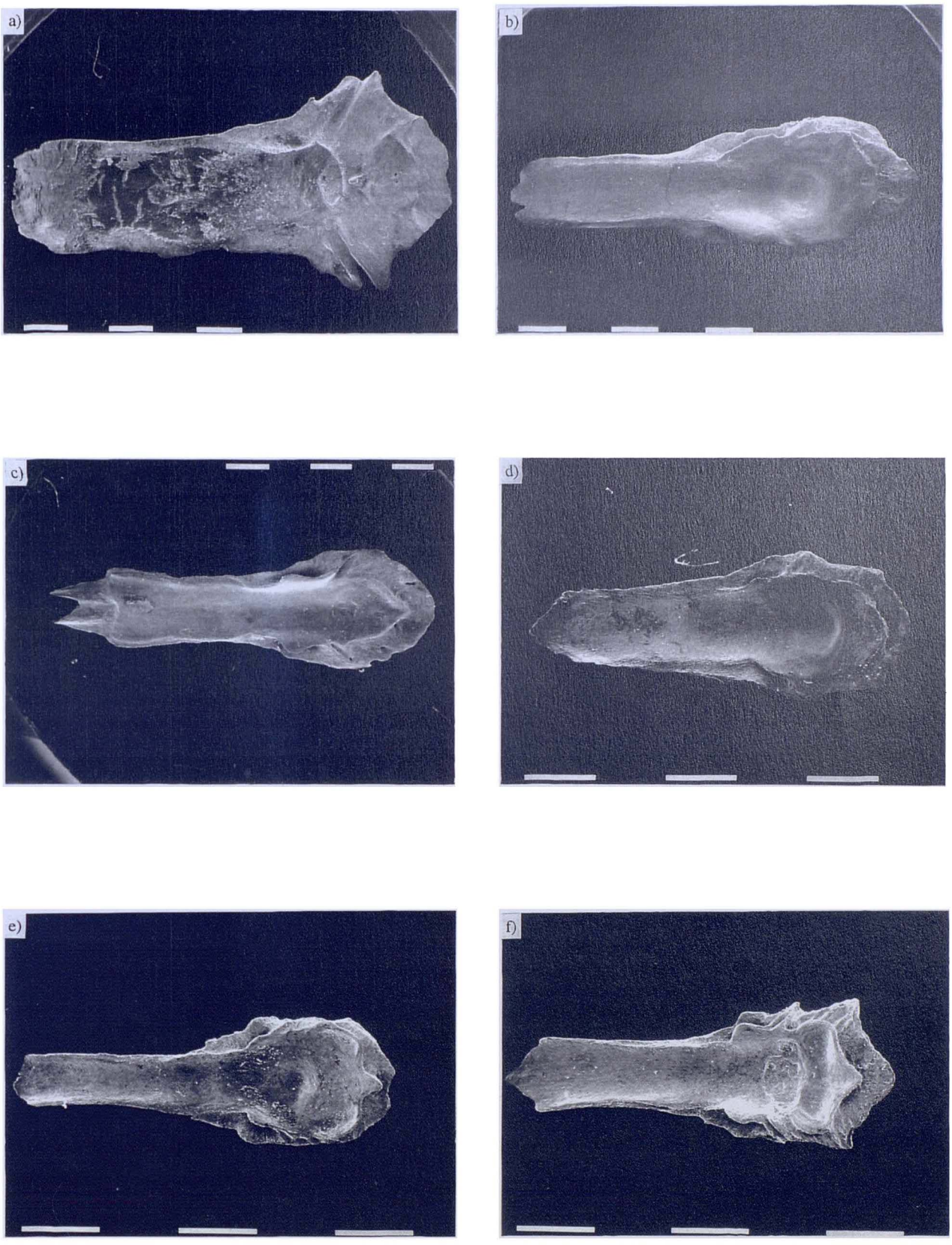


Figure 5.2 : Parasphenoids (dorsal view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

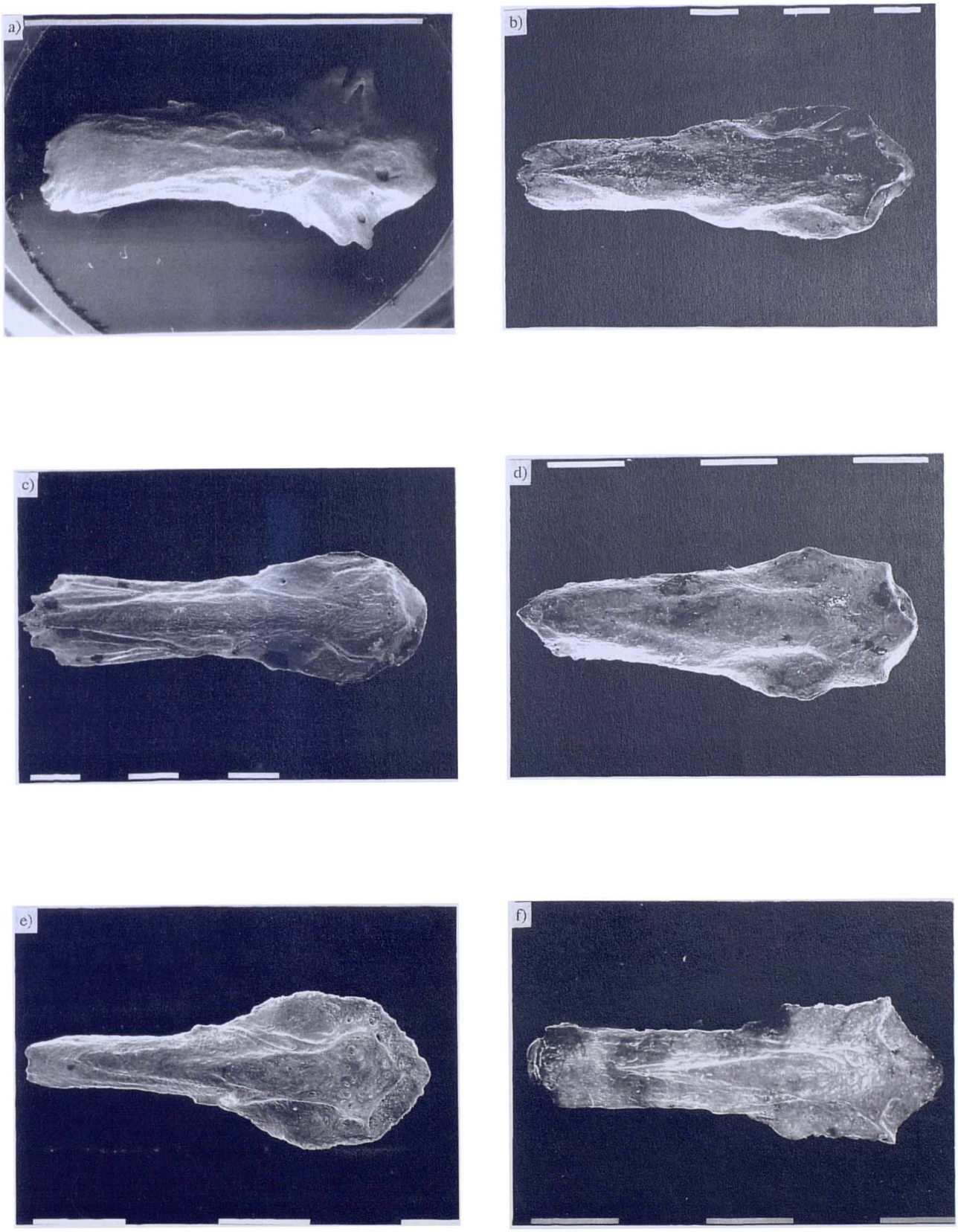


Figure 5.3 : Parasphenoids (ventral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

indented, whereas in *T. vulgaris* they are much more smoothly convex overall. The relatively shorter posterior region and narrower anterior region in *T. vulgaris* separates it from *T. marmoratus*. *T. alpestris* has quite a distinctive parasphenoid, with smoothly tapering sides between the posterior and anterior regions. Unlike in *T. vulgaris* and *T.helveticus*, the anterior tip is the narrowest point of the bone in *T. alpestris*. The posterior region is also diagnostic. Whereas *T. vulgaris* has parallel sides and *T. helveticus* is widest at its posterolateral corners, *T. alpestris* is widest laterally.

Parietals

Whereas the frontals and parietals are fused in anurans, they remain separate in salamandrids. The SEM photographs in Figure 5.4 demonstrate the typical characters of each species well. The parietals of *T. cristatus* and *T. marmoratus* can be separated from the three smaller species by their more elongate anterior portion. Any specimens of over 3.5mm in length must also belong to one of the three larger species. The acute anterolateral corners of *S. salamandra* separate it from *T. alpestris*. It is difficult to assess the possible variation within *T. cristatus* and *T. marmoratus*, but the shape of the lateral edge appears to be diagnostic. In *T. marmoratus*, the processus prooticalis is well-rounded and does not extend laterally beyond the processus occipitalis. In *T. cristatus*, the processus prooticalis projects further and is more angular. The anterior end of the parietal appears to be straighter and obliquely angled in *T. alpestris*. Diagnostic characters for separating *T. vulgaris* and *T. helveticus* have not been found.

Frontals

S. salamandra is easily separated from the newts by its thinner frontals which have an irregular subovoid outline with no ornamentation. *T. marmoratus* and *T.cristatus* have subrectangular frontals which are well ornamented on their dorsal surface (see Figure 5.5). In *T. cristatus,* the anterior region, which connects with the nasals, is most furnished with a rugose system of ridges and fossae. There also tend to be small lateral projections in this area which make the bone widest anteriorly. In *T. marmoratus*, the posterolateral corners (which connect with the parietals) project posterolaterally as acute spines, making this region the widest. The frontals are subrectangular in *T. alpestris*, but have a fairly smooth dorsal surface. The frontals of *T. vulgaris* and *T. helveticus* have a roughly triangular shape and are fairly similar, but the posterolateral corner provides a reliable means for diagnosis. Both species have distinct projections directed posterolaterally (as in *T. marmoratus* but more extensive), forming an incomplete frontosquamosal arch. This is thought to be a defensive structure to protect the eyes in some species (Naylor, 1978b). In *T. vulgaris* it is acutely angled, but relatively unextensive. In *T. helveticus*, the projection is much longer and extends to be the posteriormost part of the bone. Thus, in the living animal, the bony frontosquamosal arch is continuous in *T. helveticus* but discontinuous in *T. vulgaris*.

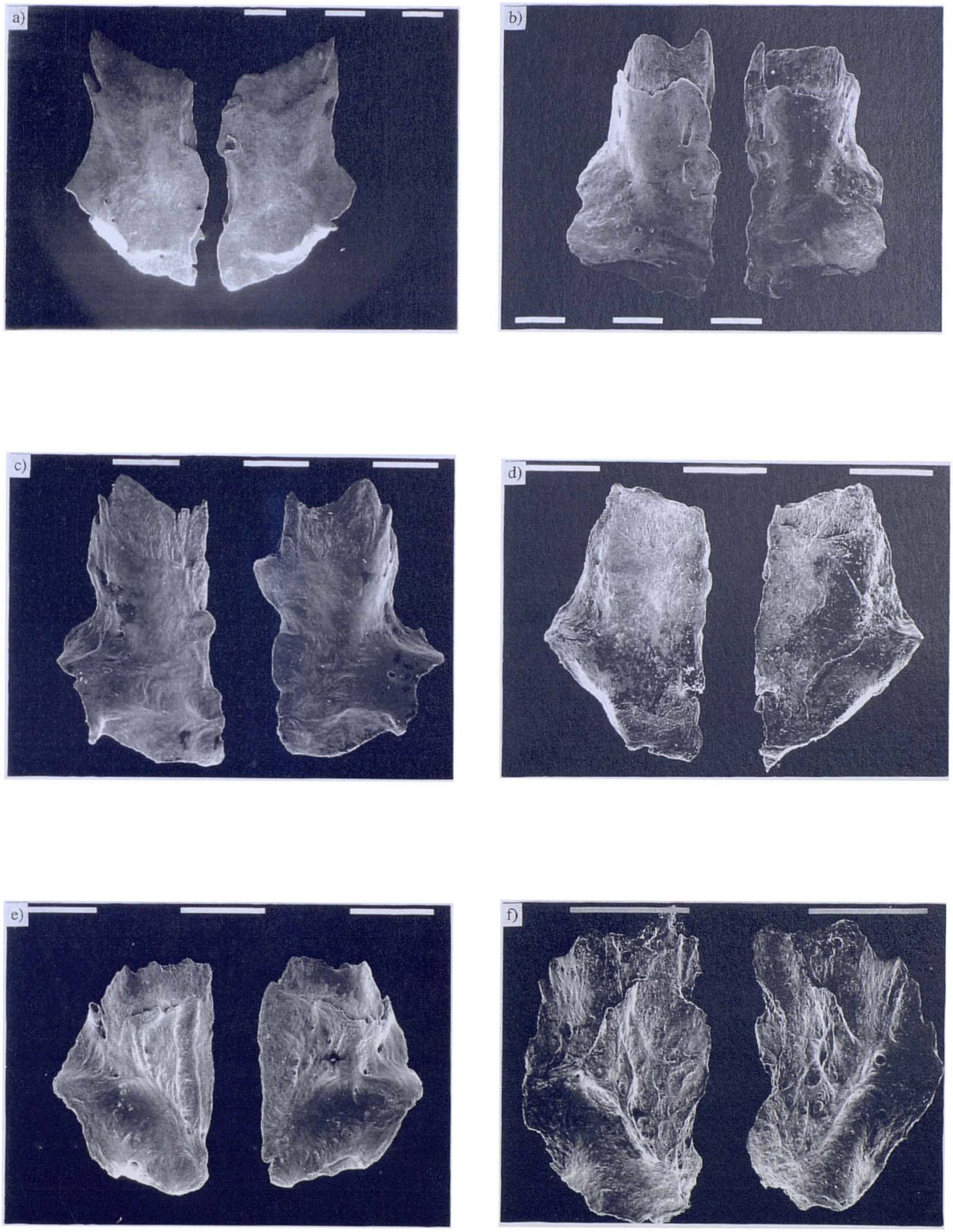


Figure 5.4 : Parietals (dorsal view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

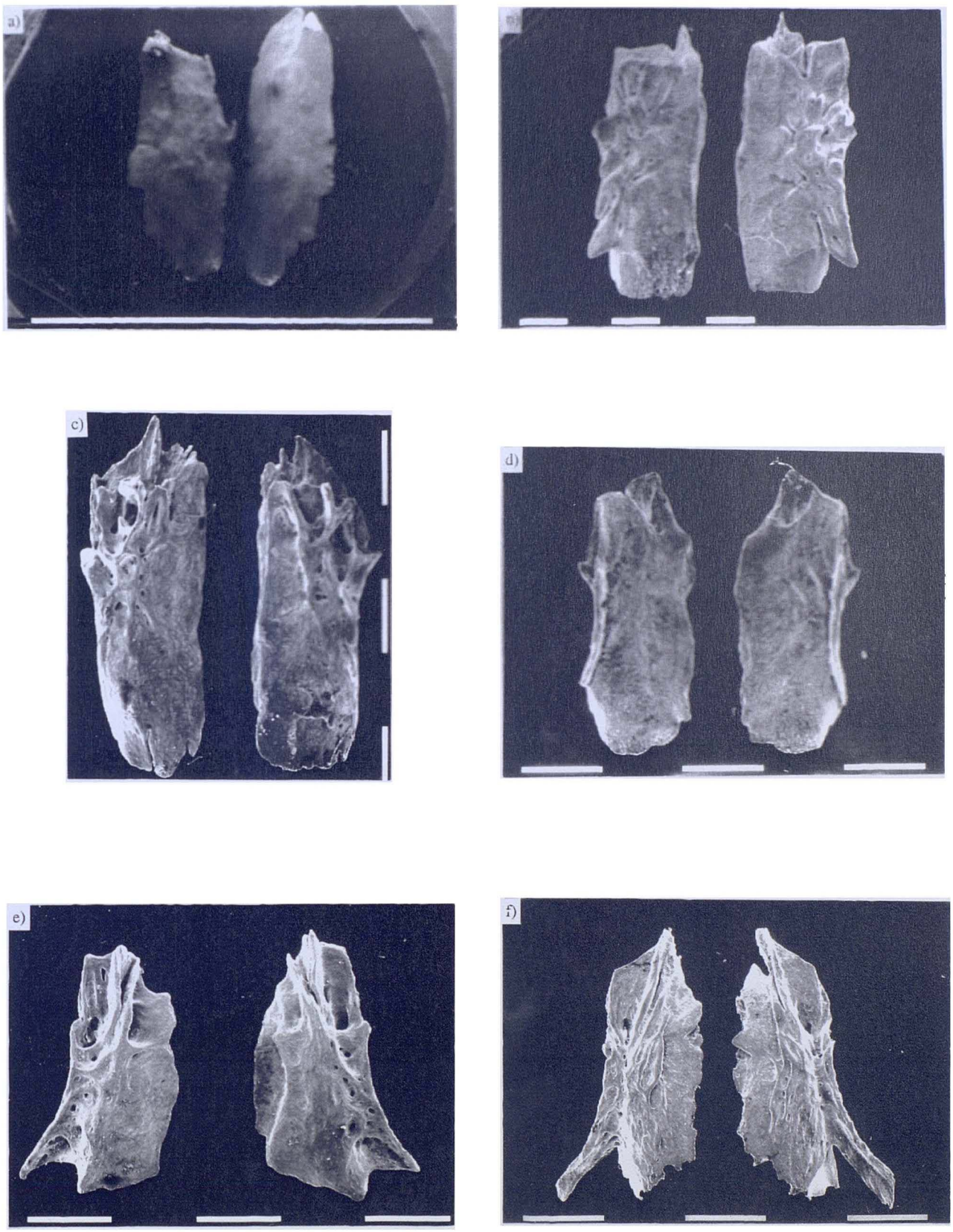


Figure 5.5 : Frontals (dorsal view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

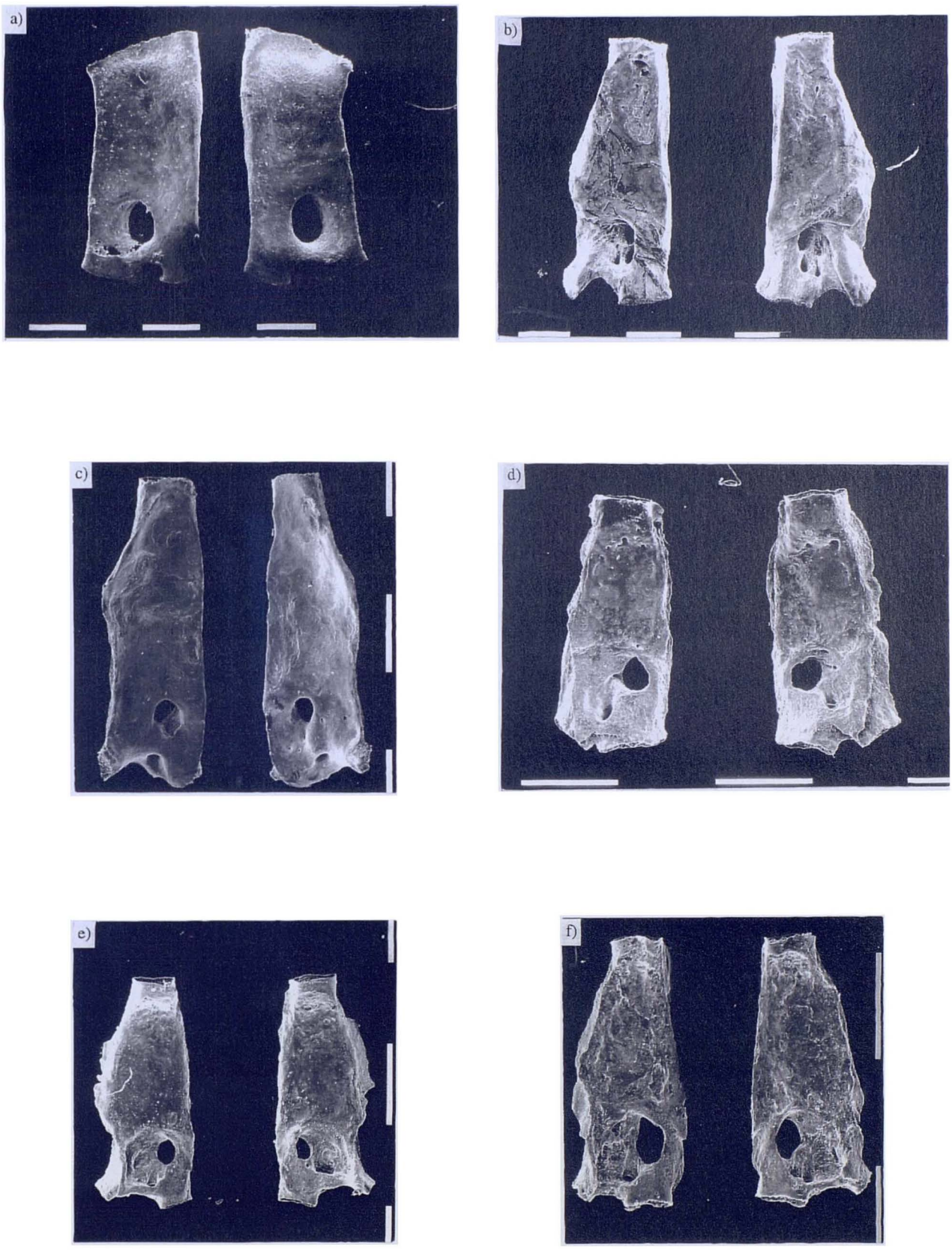


Figure 5.6 : Orbitosphenoids (medial view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

Orbitosphenoids

Each orbitosphenoid is a subrectangular plate with a rounded fenestra towards its posterior end (Figure 5.6). *S. salamandra* can be distinguished easily as its anterior end is as wide as the posterior end, whereas in *Triturus* it is narrower. *T. cristatus* can be diagnosed by its more elongate form. The other four species of *Triturus* considered here are difficult to tell apart, especially as the potential variability of this bone is not known fully.

Prootic-exoccipital

These paired bones, known collectively as the otoccipital by Duellman and Trueb (1986), form the posterior part of the braincase and the foramen magnum. Their shape appears to be quite distinctive, but is difficult to describe without initiating complex terminology. The SEM photographs provided (Figure 5.7) can probably be used as reliable keys, and visual comparison would be simpler than description here.

Premaxilla(e)

These are upper jaw elements and house a row of tiny pedicellate teeth, each in an individual socket. Wake and Özeti (1969) considered the fusing of the premaxillae to be a derived state, and that paired premaxillae were to be found in primitive salamandrid species. In *S. salamandra,* the premaxillae are paired, immediately separating them from *Triturus* species (see Figure 5.8). In *Triturus* there is a single (fused) premaxilla with a bifurcating dorsal projection which forms the medial walls of the olfactory capsule above. These projections tend to remain partly fused or closely parallel to each other in *T. marmoratus* and *T. cristatus*, but are more divergent in the three smaller species. The general larger size of the former species should also allow their distinction. *T. alpestris*, *T. vulgaris* and *T. helveticus* can probably not be easily differentiated using this element.

VERTEBRAE

The vertebral column consists of around 45 to 50 individual vertebrae in *Triturus*, though there can be some variation in the number of caudal vertebrae and perhaps trunk vertebrae (Halliday, pers. comm.). There appear to be characteristic size/shape configurations for different parts of the vertebral column. However, these are very small and intricate elements which are often subtly assymmetrical and variable in other ways. Trunk vertebrae possess bifurcated transverse processes. These connect to a single rib on each side. Each rib has a bicapitate proximal articulation, tapering to an acute distal tip which is angled ventrolaterally and posterolaterally.

Atlas vertebra

Salamandrids have a distinctive atlas, with a paired anterior articulation to connect with the occipital condyle, and a rounded, steeply sloping anterior face. Diagnostic criteria have not been isolated for this element. It is found less frequently as a fossil than the more numerous trunk vertebrae.

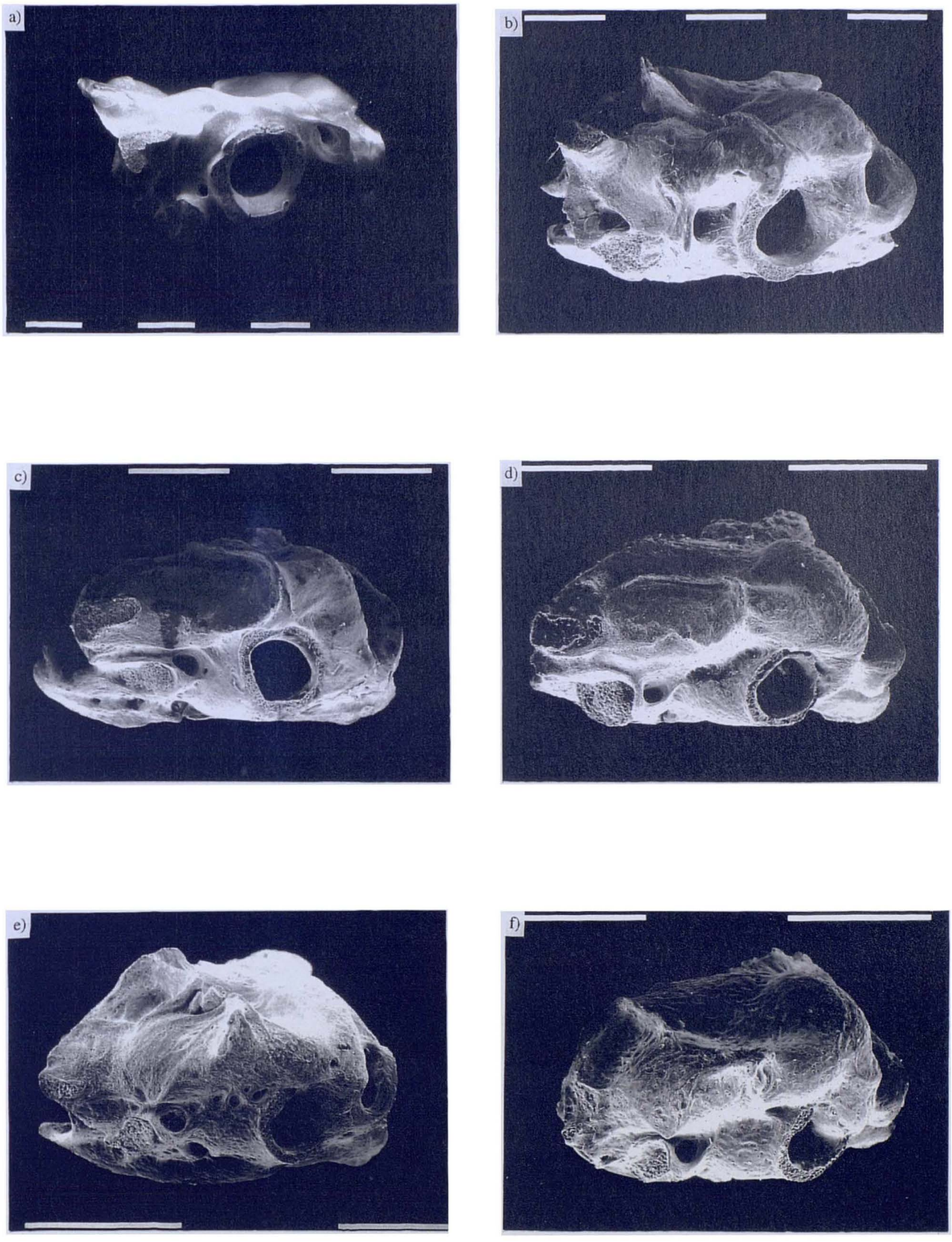


Figure 5.7 : Left prootic-exoccipital (lateral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

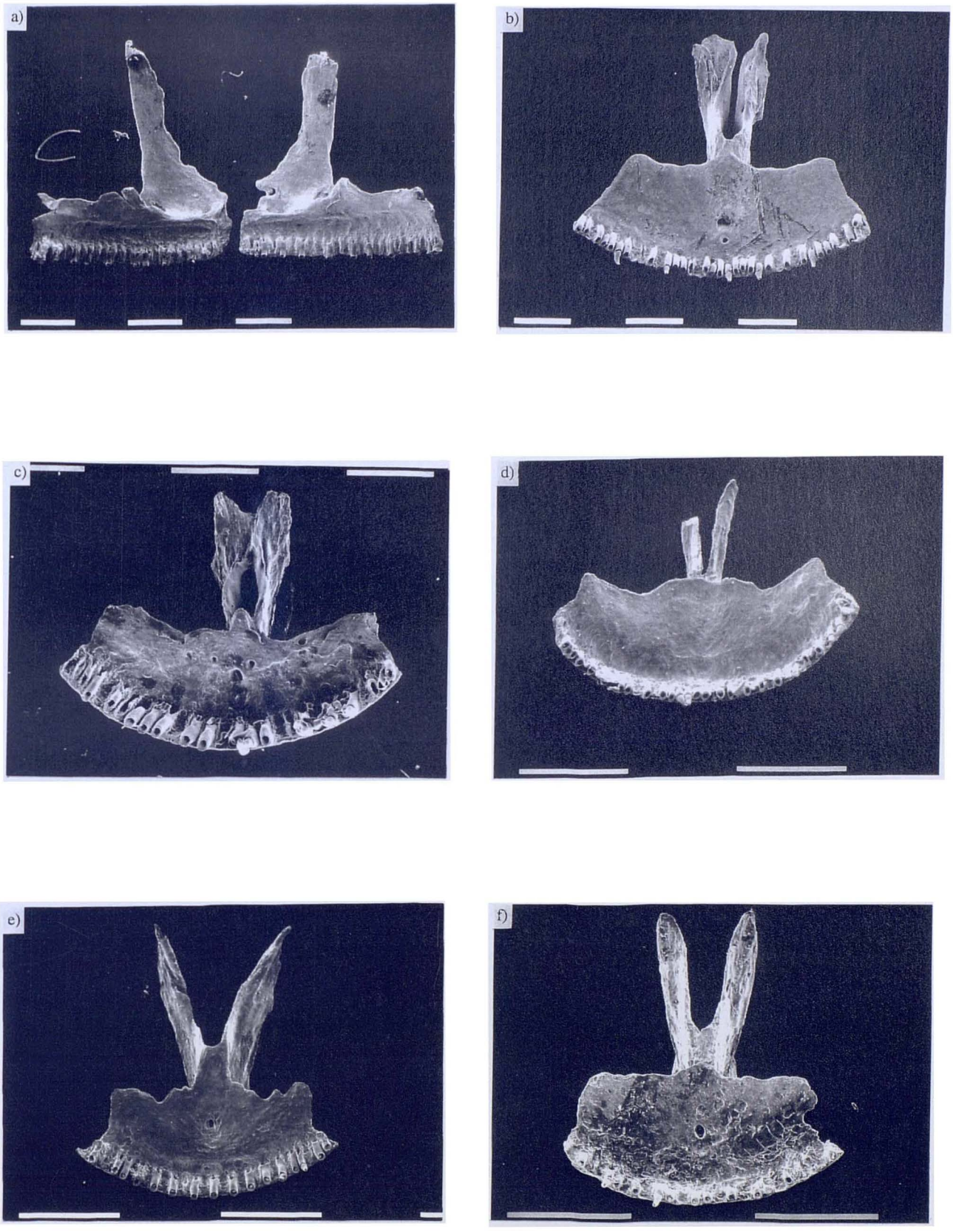


Figure 5.8 : Premaxilla(e) (posteroventral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

Trunk vertebrae

The second (axis) vertebra can be distinguished as it is shorter than the other trunk vertebrae and has a much smaller anterior articulation, equivalent to the odontoid peg in mammals. The third and fourth vertebrae can be separated on the basis of their shorter length and relatively larger neural canal. Their diapophyses are noticeably flared, and short in relation to the height of the neural spine. The distal ends of the diapophyses form wide articulations, suggesting connection to sturdier ribs, perhaps anterior to the pectoral girdle. Strictly speaking, these are cervical vertebrae, but as they bear ribs they are considered trunk vertebrae here. Duellman and Trueb (1986) class all vertebrae between the atlas and sacral region as trunk vertebrae for this reason.

The fourteen or so trunk vertebrae are overall very similar in shape, but their position in series could be identified on other features such as relative proportions, centrum length or on the arrangement of the transverse processes. Overall size and relative proportion allows distinction between some of the species studied. Trends in finer details do allude to an overall general character for each species. However, the level of intracolumnar variation and differences between specimens makes diagnosis more difficult between some species. One or two trunk vertebrae have very wide, narrow and slightly convergent diapophyses. These appear to be positioned in the posteriormost section of the trunk region (in front of the sacral vertebrae), perhaps with a ligament connection to the pelvic girdle which is not obviously articulated in any way with the sacral vertebrae. The underside in all trunk vertebrae has a framework of ventral laminae, reinforcing the perpendicular components of the vertebra. From anterior view, their leading edges appear like platforms between the lower diapophyses and the anterior part of the centrum.

Specific identification using vertebrae is generally possible for the species studied. The *S. salamandra* specimen studied has much wider and more robust vertebrae than *Triturus* (see Figures 5.9-5.13). The vertebrae are vertically compressed, with a low neural crest, and are wider than any species of *Triturus* seen. In anterior view (see Figure 5.11), the centrum of *S. salamandra* appears wider, and the transverse processes are more streamlined. However, Hodrová (1984) illustrated Pliocene specimens from Central Europe which are much narrower. Interestingly, a related Miocene species of *Salamandra*, described by Herre (1955), has very wide vertebrae. Rage (1974) also illustrated a *S. salamandra* vertebra.

The vertebrae of *T. cristatus* and *T. marmoratus* are relatively longer than *T. alpestris*, and both longer and more slender than *T. vulgaris* and *T. helveticus*. The two larger species have correspondingly longer vertebrae than the others (>3.5mm in adults, as opposed to <3mm). *T. alpestris* has relatively narrow vertebrae, with a more elongate appearance than *T. vulgaris* or *T. helveticus*.

The neural spine is much higher and stronger in *T. marmoratus* than in *T. cristatus* where it is low and often discontinuous, being most prominent mid-length. It is high in the three smaller species. *T. marmoratus* has a high continuous neural crest which bifurcates posteriorly, creating a V-shaped notch in the roof of the neural arch. In mature specimens, the trunk vertebrae are easily

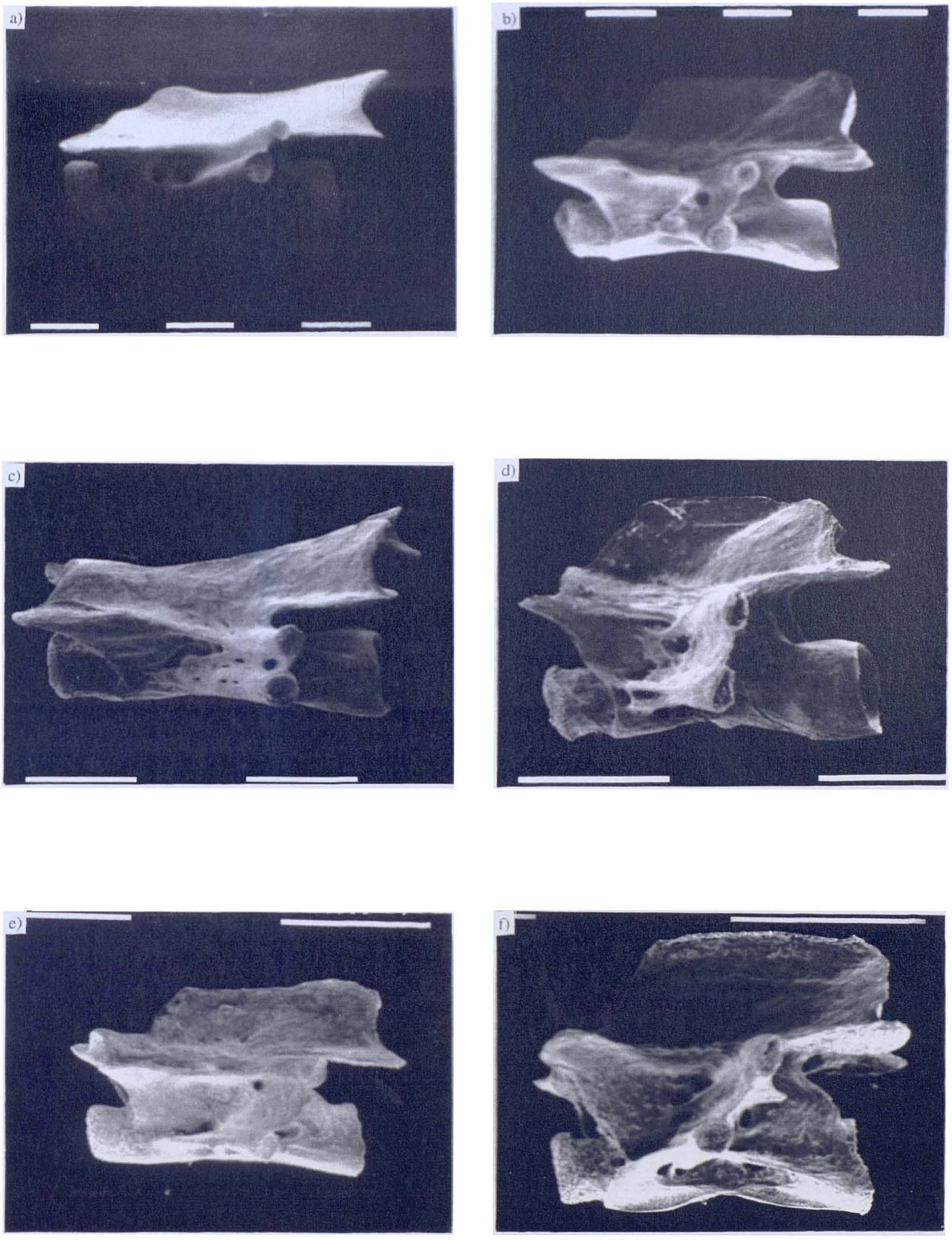


Figure 5.9 : Trunk vertebra (left lateral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

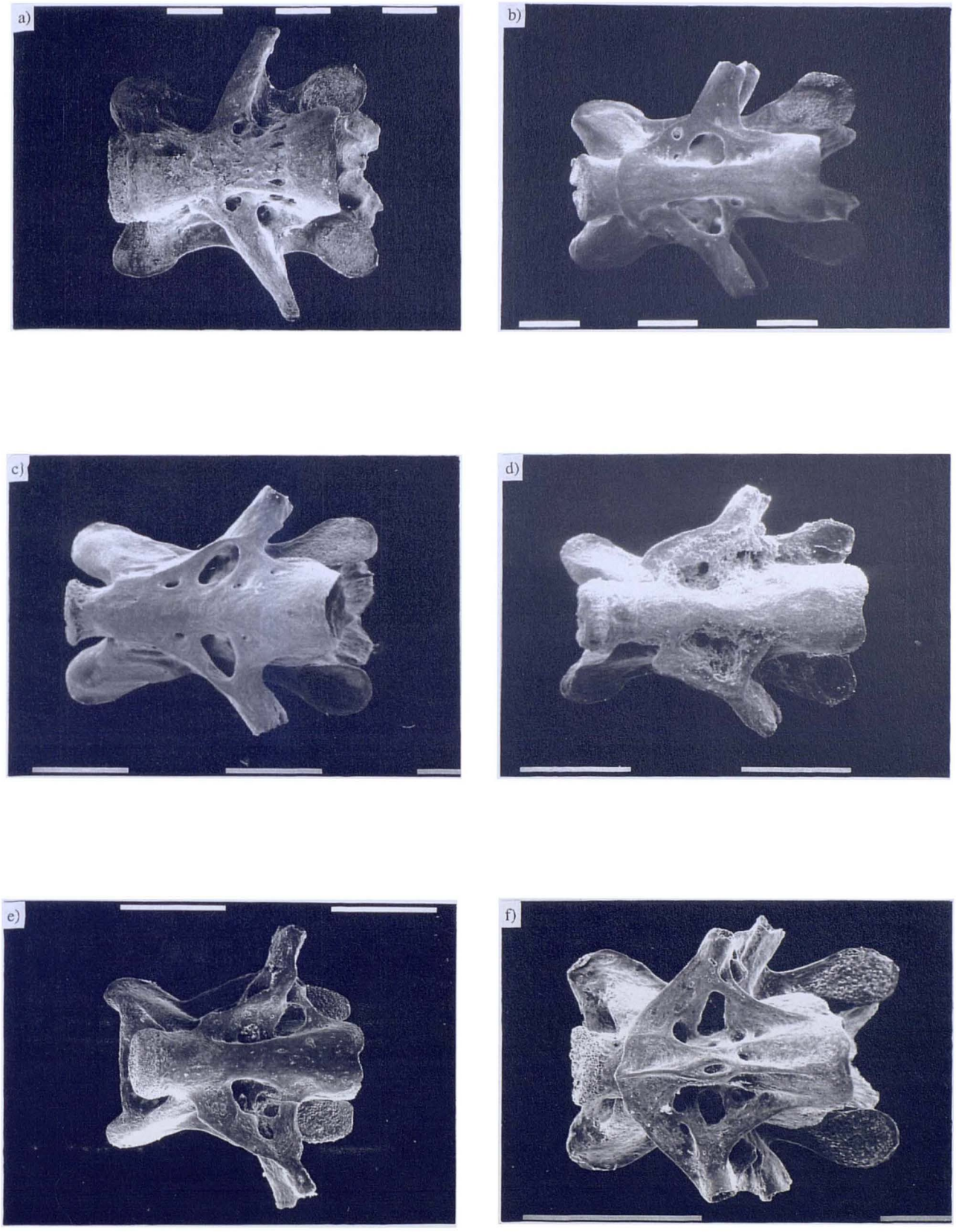


Figure 5.10 : Trunk vertebra (ventral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

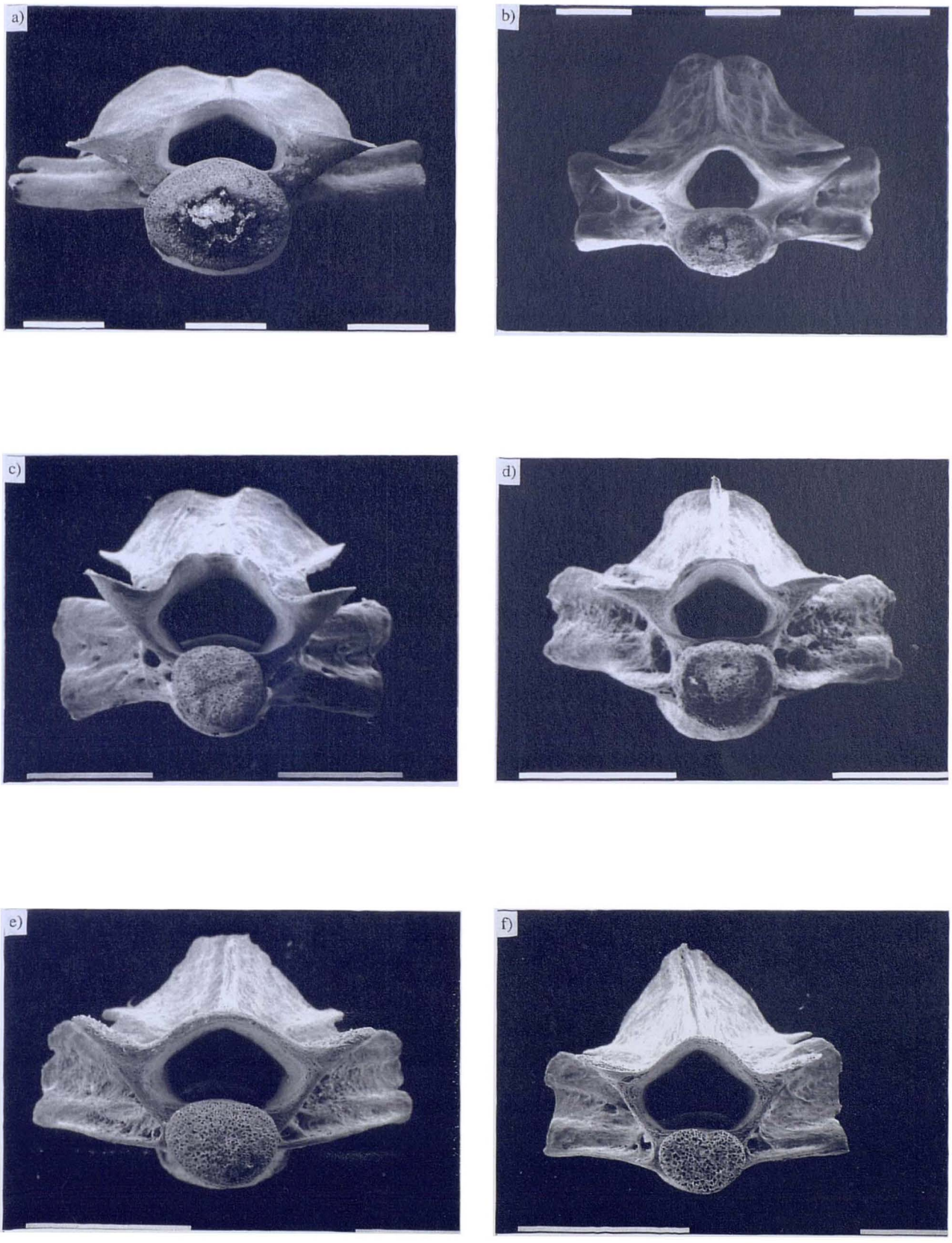


Figure 5.II : Trunk vertebra (anterior view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

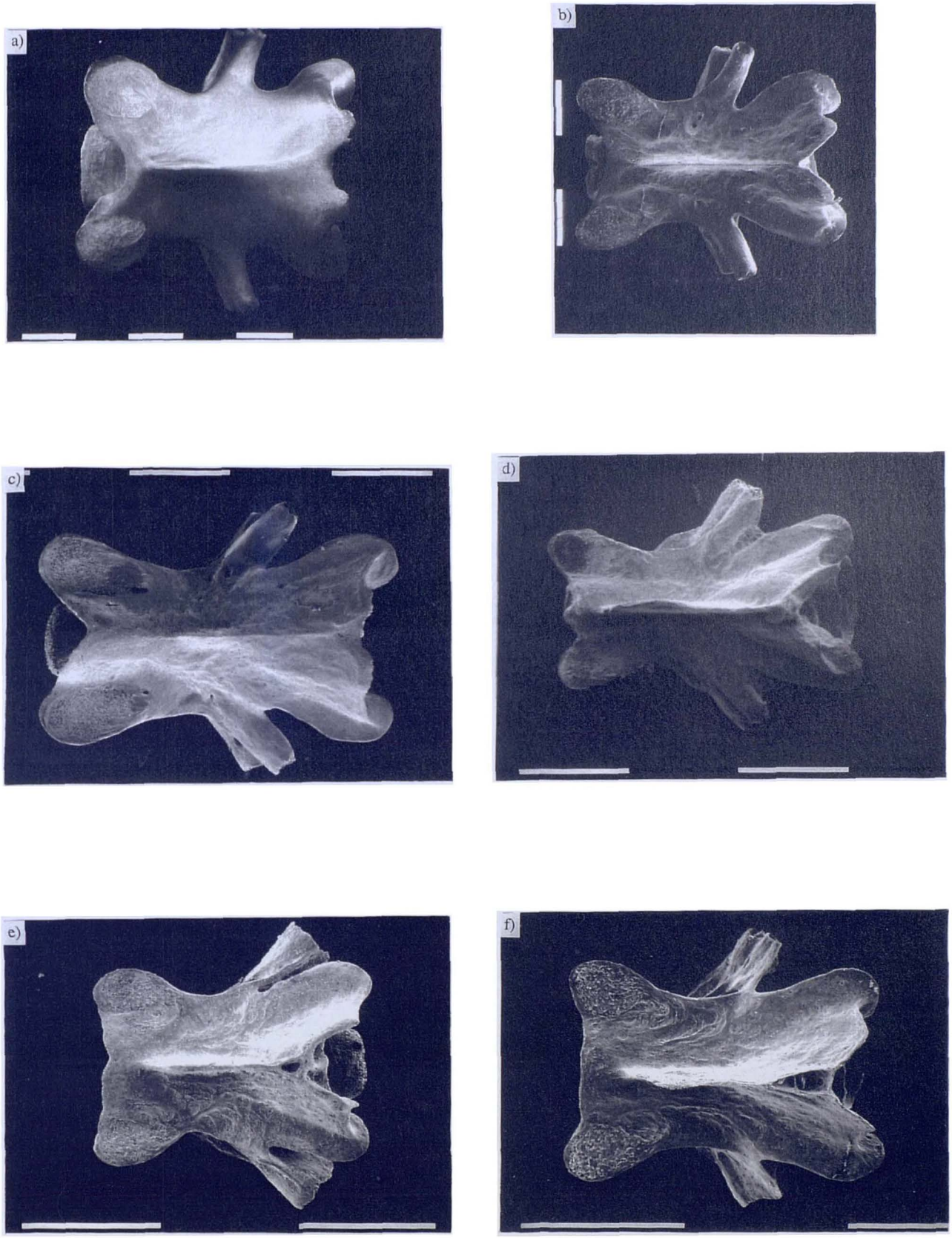


Figure 5.12 : Trunk vertebra (dorsal view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

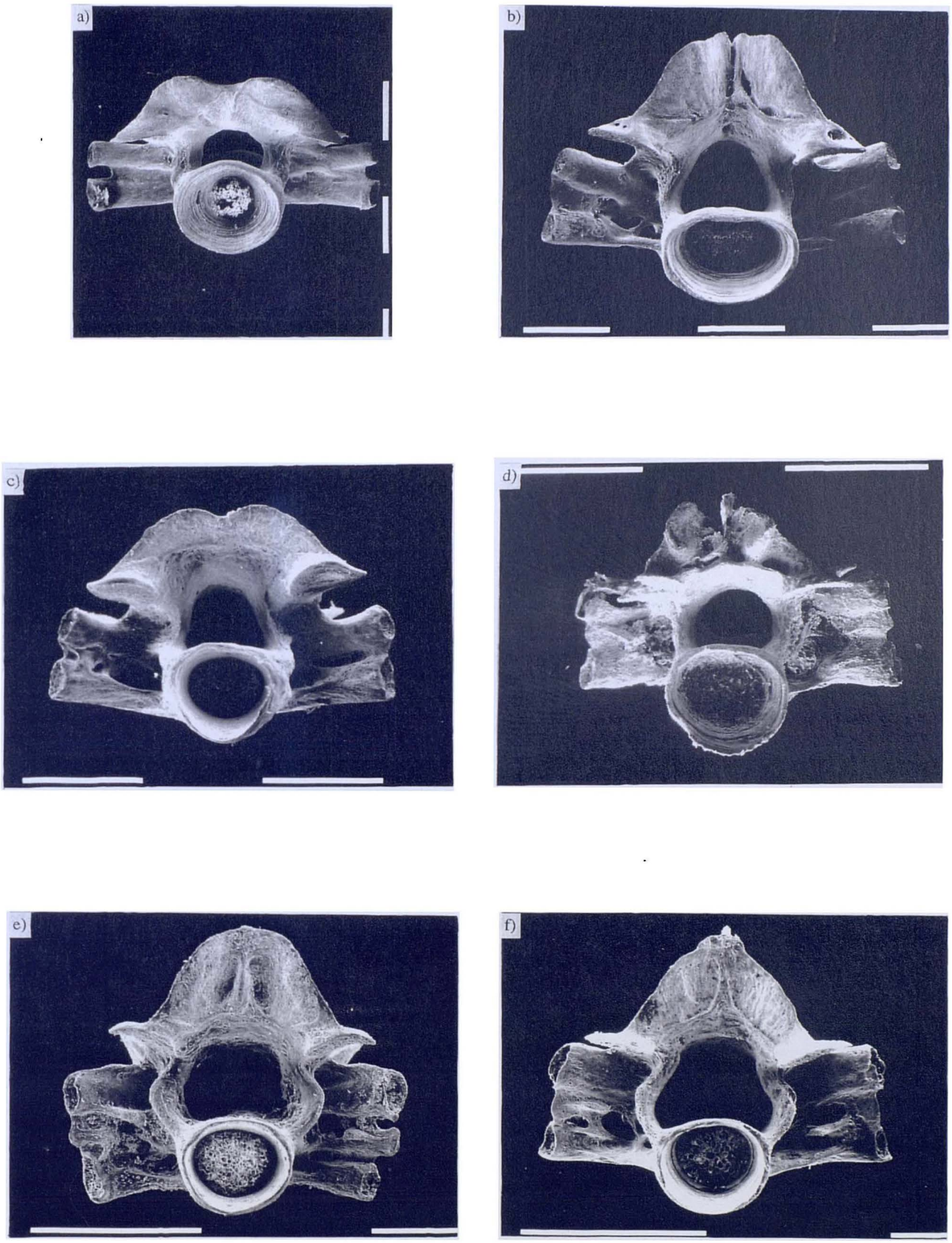


Figure 5.13 : Trunk vertebra (posterior view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

distinguished from the smaller newts due to their greater size, but in juveniles this is not possible as the trunk vertebrae of *T. marmoratus* are virtually indistinguishable from those of *T. vulgaris.* Reliable identification on specimens within the size range of *T. vulgaris* is only possible using cloacal and caudal vertebrae.

Holman and Stuart (1991) suggested that *T. vulgaris* can be separated from *T. helveticus*, when viewed dorsally, by the size of a 'U-shaped' notch in the neural arch. The notch is deeper, and perhaps more W-shaped, in *T. vulgaris* (see Figures 5.12e,f)). When viewed anteriorly (Figure 5.11), the size of this notch can be seen to relate to the slopes of the posterior neural arch ascending at different angles in the two species. The steeper angle in *T. vulgaris* creates a level platform at the apex (with a deeper notch). In *T. helveticus* the sides converge to a peak which gives the neural spine a triangular appearance in anterior view (with a smaller notch). Some specimens are not as distinctly pointed, relating to position in the vertebral column. One specimen of *T. helveticus* (CGO 21/1) has decidedly shouldered neural arch in most of its vertebrae, when viewed anteriorly. The base of the neural arch is slightly narrower than in all *T. vulgaris* specimens seen, falling well within the width of the zygapophyseal tips. Thus, there appears to be ambiguity, and confident diagnosis might not be possible in all cases. No other criteria could be found for differentiating trunk vertebrae of these two species conclusively.

Sacrum and precaudal vertebrae

The sacrum is distinguished from the preceding vertebrae by its fenestrate ventral process. This takes the form of a rectangular frame, often discontinuous at one ventro-lateral corner. Its neural spine is otherwise like that of a trunk vertebra. The ventral process is posteriorly-directed and is larger in females. The two succeeding precaudal vertebrae also have a large ventral process, though without the fenestra. This is clearly hollow when viewed posteriorly. They are transitional in form between trunk and caudal vertebrae and share the same diagnostic features described above for trunk vertebrae. Of interest also: from the specimens studied, it appears that *T. vulgaris* normally possesses fifteen trunk vertebrae, whereas there are fourteen in *T. helveticus.*

Caudal vertebrae

The sacrum and precaudals are succeeded by up to thirty or so caudal vertebrae. These are variable in number in *Triturus* with a highly intricate structure and some intracolumnar variation. They exhibit few obvious consistencies to characterise each species. As well as an exaggerated neural spine, the caudals possess a bulbous haemal arch which extends into a ventral process.

The caudal vertebrae of *S. salamandra* are easily distinguished from *Triturus* as they have much reduced neural and haemal spines (see Figures 5.14 and 5.15). In *T. cristatus*, these dorsal and ventral processes are larger but relatively shorter and more streamlined than the other *Triturus* species. They are longer in *T. marmoratus*, well-rounded in lateral profile, and of similar proportions to *T. vulgaris.* The anterior end of the haemal arch is also constricted in *T.*

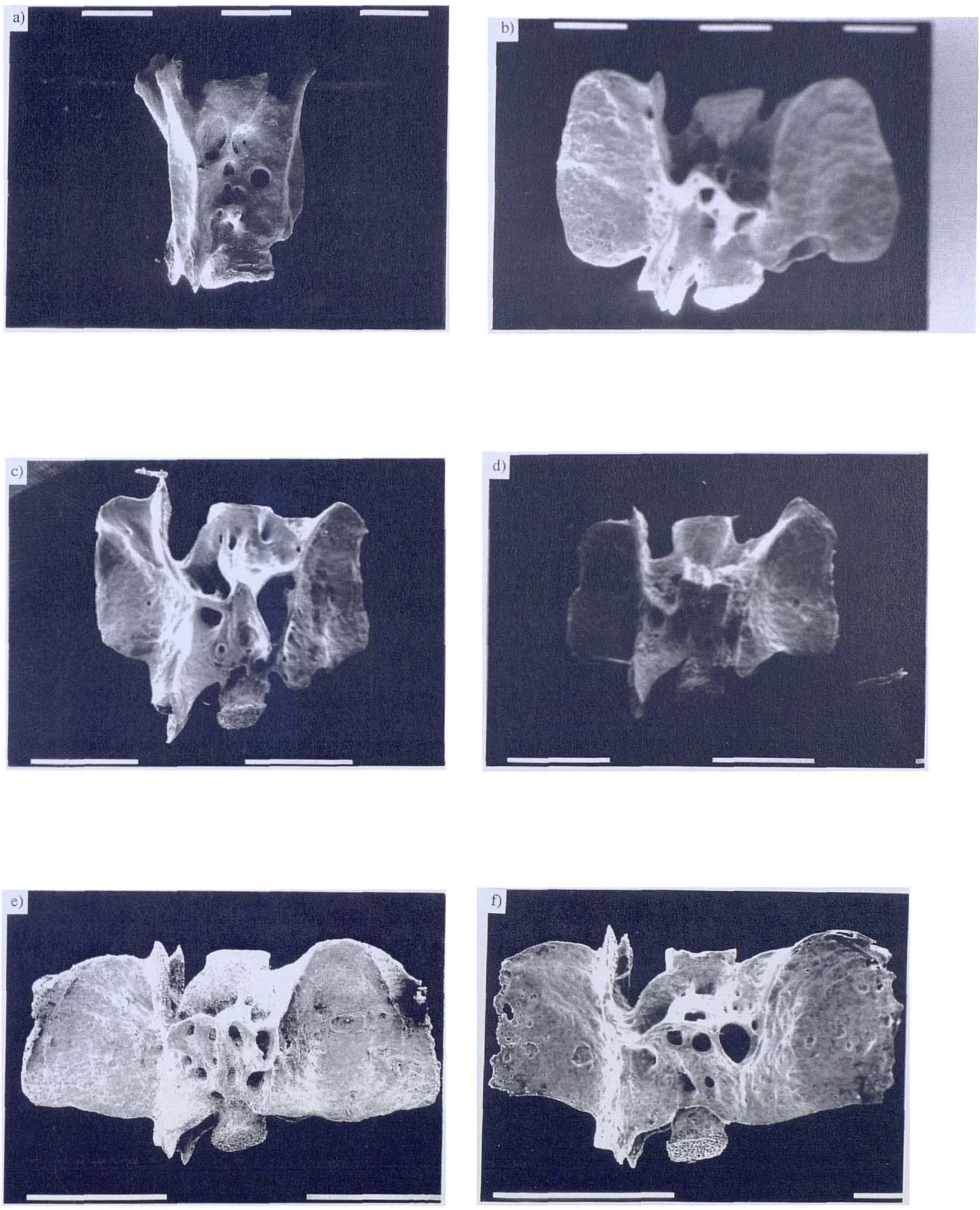


Figure 5.14 : Caudal vertebra (left lateral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

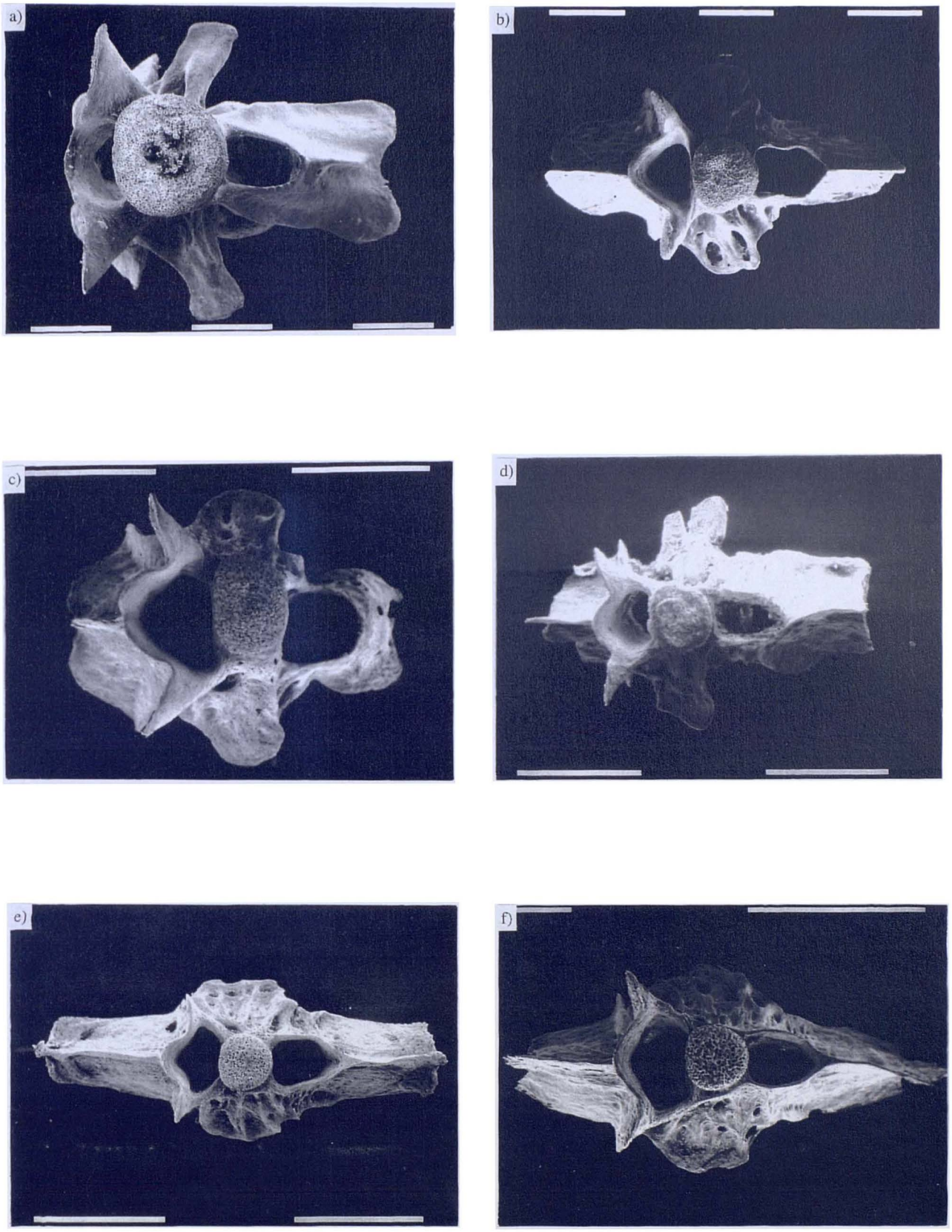


Figure 5.15 : Caudal vertebra (anterior view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

marmoratus, giving it the appearance of a key-hole. For immature *T. marmoratus*, this may be useful in distinguishing caudal vertebrae from those of *T. vulgaris* and *helveticus*. The tips of its neural and haemal spines are fairly angular.

Of the smaller species, *T. vulgaris* and *helveticus* have much narrower and longer neural and haemal spines. When viewed anteriorly, these are seen as fin-like projections extending from the vertically exaggerated neural and haemal arches. Their tips in *T. helveticus* have a very acute angular profile, whereas *T. vulgaris* has rounded or square crests (cf. trunk vertebrae). It appears also that these features may be variable in height for male specimens of *T. helveticus,* possibly induced by seasonal tail enlargement. Such features are probably too delicate to be preserved in fossils. *T. alpestris* has much shorter vertical features, similar to those of *T. cristatus*, but much narrower in anterior aspect.

PECTORAL GIRDLE

Scapulocoracoids

These are fairly consistent in shape and can offer some diagnostic information (see Figure 5.16). In *S. salamandra*, the coracoid portion of the bone is small in relation to the scapula portion, whereas in the coracoid is large and forms a broad semicircular fan. The scapula part is widely flared in *T. cristatus*, but less so in *T. marmoratus*. The three smaller species have a scapula region which is formed by two tubular extensions, connected by a thin lamina. This separates them from the *cristatus* group, but diagnosis of individual species has not been possible.

PELVIC GIRDLE

The salamandrid pelvic girdle consists of paired fused bones representing the ischium and pubis, fomred of roughly rectangula plates. These do not appear to be too well ossified, and probably do not preserve in fossil assemblages. However, the elongate ilia are more robust.

Ilium

The ilia are elongate, and cylindrical in form, eith a cup-shaped acetabulum. From size differences, it is possible to separate the larger *Triturus* from the smaller species, but shape differences have not been found to be diagnostic. *S. salamandra* has a fairly distinct ilial shape, as illustrated by Rage (1974), with a more widely flared proximal end than in *Triturus*.

APPENDICULAR SKELETON

See Figure 5.17 for overall form. The limb elements in newts are relatively featureless and not conclusively distinguishable between species. Nevertheless, *S. salamandra* can normally be separated with relative ease. The larger *cristatus* group (*T. marmoratus* and *T. cristatus*) can, in some cases, be separated from the smaller *vulgaris* group (*T. alpestris, T. vulgaris* and *T. helveticus*). Rage (1974) illustrated the femur and humerus of Quaternary fossil *S. salamandra.*

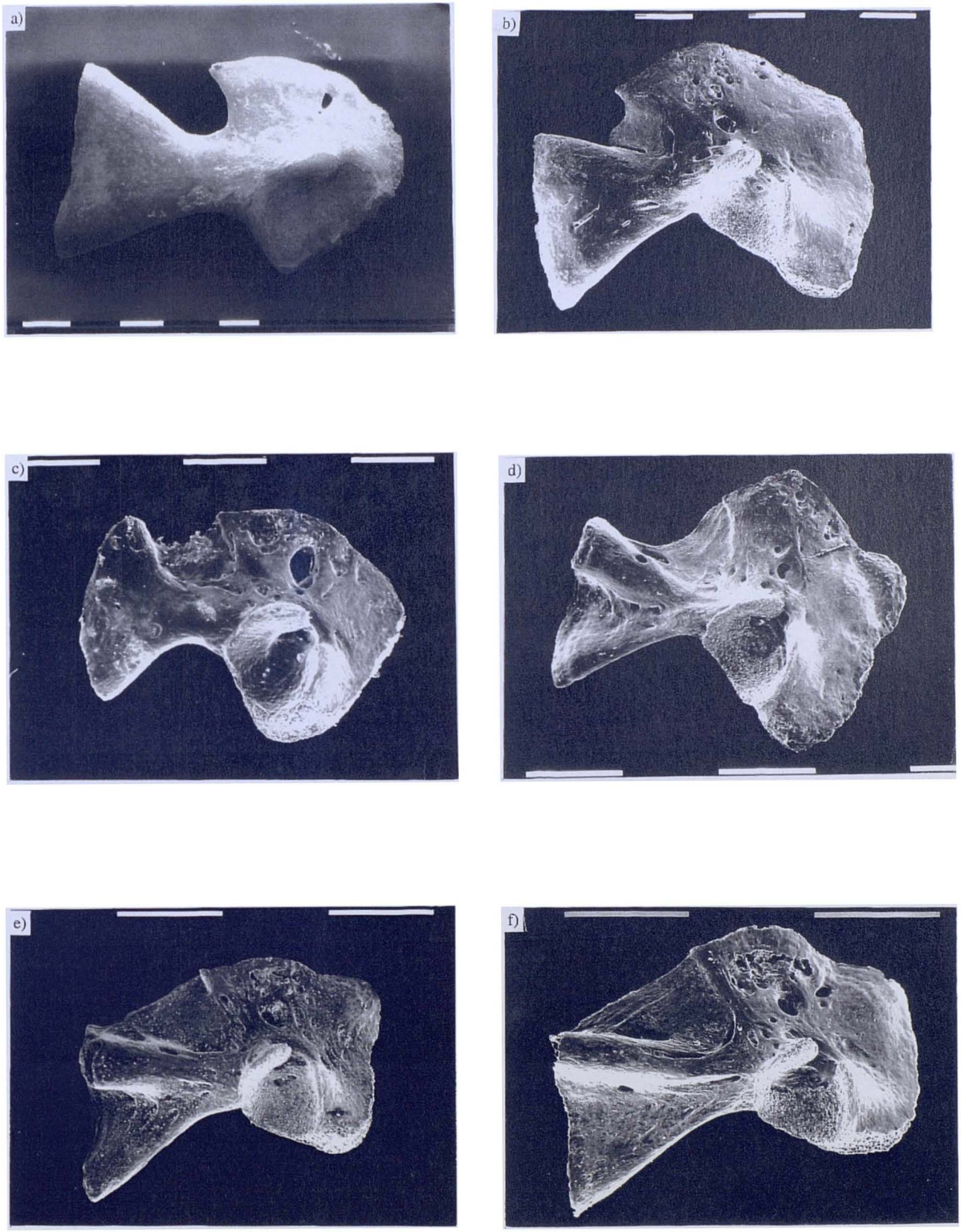
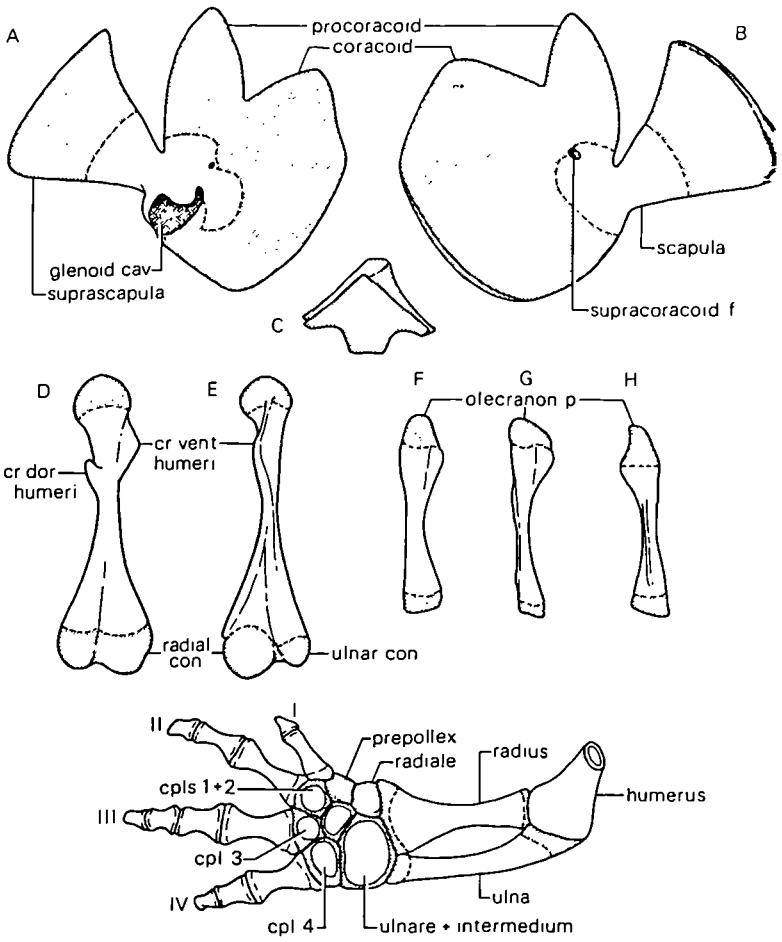


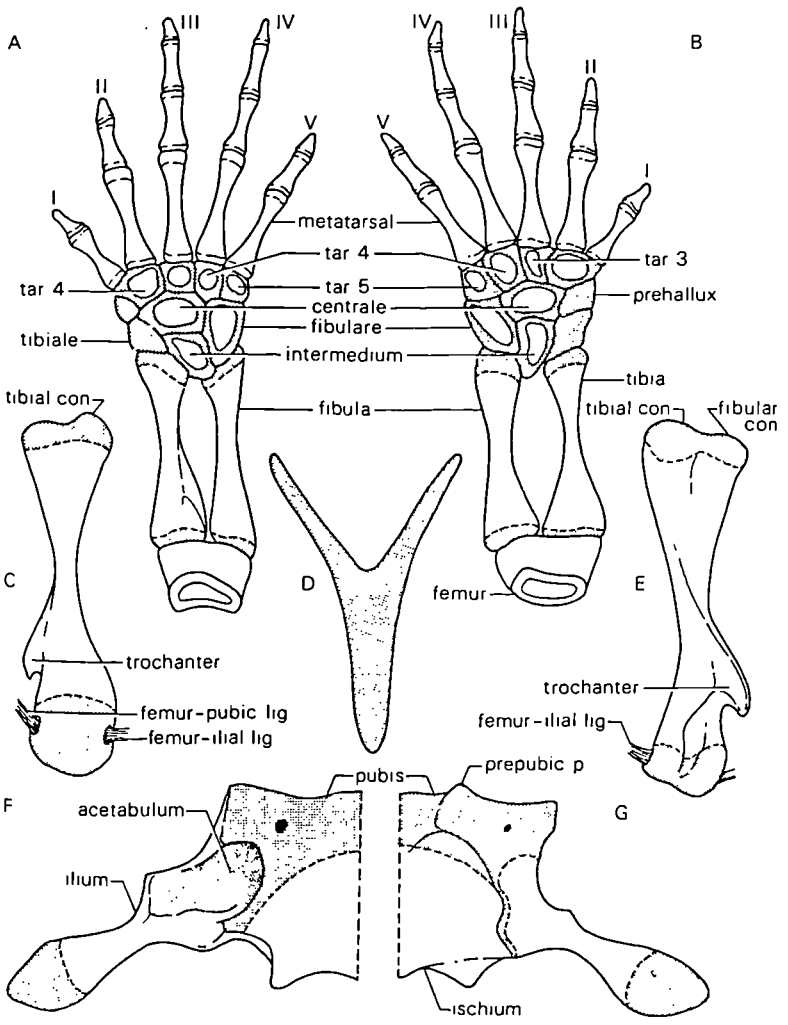
Figure 5.16 : Right scapulocoracoid (ventrolateral view) of: a) *S. salamandra*; b) *T. marmoratus*; c) *T. cristatus*; d) *T. alpestris*; e) *T. vulgaris*; f) *T. helveticus*.

a)



Anterior appendicular skeleton of *Salamandra salamandra*, redrawn from Francis (1934). **A.** Right half of pectoral girdle in ventrolateral view and **B.** dorsomedial view. **C.** Ventral aspect of sternum. **D.** Right humerus in dorsal aspect and **E.** ventral aspect. **F.** Right ulna illustrated from dorsal, **G.** postaxial, and **H.** ventral surfaces. **I.** Left forearm and hand in dorsal view. Cartilage is stippled. Abbreviations: cav = cavity; con = condyle; cpl(s) = carpal(s); cr = crista; dor = dorsalis; f = foramen; p = process; vent = ventralis.

b)



Posterior appendicular skeleton of *Salamandra salamandra*, redrawn from Francis (1934). **A.** Dorsal view of right foot. **B.** Ventral view of right foot. **C.** Extensor surface of right femur. **D.** Ventral aspect of ypsiloid cartilage. **E.** Flexor surface of right femur. **F.** Pelvic girdle in ventrolateral and **G.** dorsomedial (G) aspects. Cartilage is in stippled pattern. Abbreviations: con = condyle; lig = ligament; p = process; tar = tarsal.

Figure 5.17: Appendicular skeleton of *S. salamandra*: a) Scapulocoracoid and forelimb; b) hindlimb and left half of pelvic girdle (after Duellman and Trueb, 1986).

Humeri

The humeri of *S. salamandra* can be easily separated from *Triturus* by their more robust and sturdier form (see Figure 5.17a). They have a very widely flared proximal end and the crista ventralis is much wider than in *Triturus*. Humeri of the *cristatus* group species are longer and relatively more slender than those of the *vulgaris* group. The crista ventralis is not markedly elongated as suggested by Holman and Stuart (1991), hence this feature is unreliable as a diagnostic criterion. A better guide is the more robust form of the crista dorsalis in *T. cristatus* compared to the narrow and delicate projection in the smaller newts. Also, in the *vulgaris* group the diaphysis is relatively thinner in comparison with its distal expansion. *T. cristatus* humeri can be broadly flared and flattened proximally.

Femora

The femora of *S. salamandra* are much more robust and wider at their ends than in *Triturus* (see Figure 5.17b). The larger *cristatus* group have longer and more robust femora than the *vulgaris* group. They are also elongated proximally, as suggested by Holman and Stuart (1991). However, these elements are insufficiently reliable for specific identification, particularly as immature *cristatus* group specimens may be confused with the *vulgaris* group.

Radii, ulnae, tibiae and fibulae

These are easily recogniseable as such and are sometimes found as fossils, but do not exhibit obvious diagnostic characters. *S. salamandra*, however, is separable by its larger size in adult specimens. See also Figure 5.17b.

5.3 Anura

The Anura exhibit the same skeletal configuration in all families. They almost all have nine vertebrae, and all have a large skull and limbs. This is accordingly reflected in the relatively large proportions of non-vertebral anuran remains found as fossils, when compared to the Salamandridae, Sauria and Ophidia which are largely represented by vertebrae.

As skeletal character is similar within families, each of six families is considered separately in the subsequent sections. However, useful illustrations from Boulenger (1897-8), Böhme (1977) and Duellman and Trueb (1986) are reproduced together here, as they provide an overview of visual comparisons, and illustrate the form of the anuran skeleton (see Figures 5.18-5.25). Whilst it will be seen that some of the elements figured are easily identified to species level from these drawings, it is stressed that they do not constitute an identification key, and are not a substitute for real comparison.

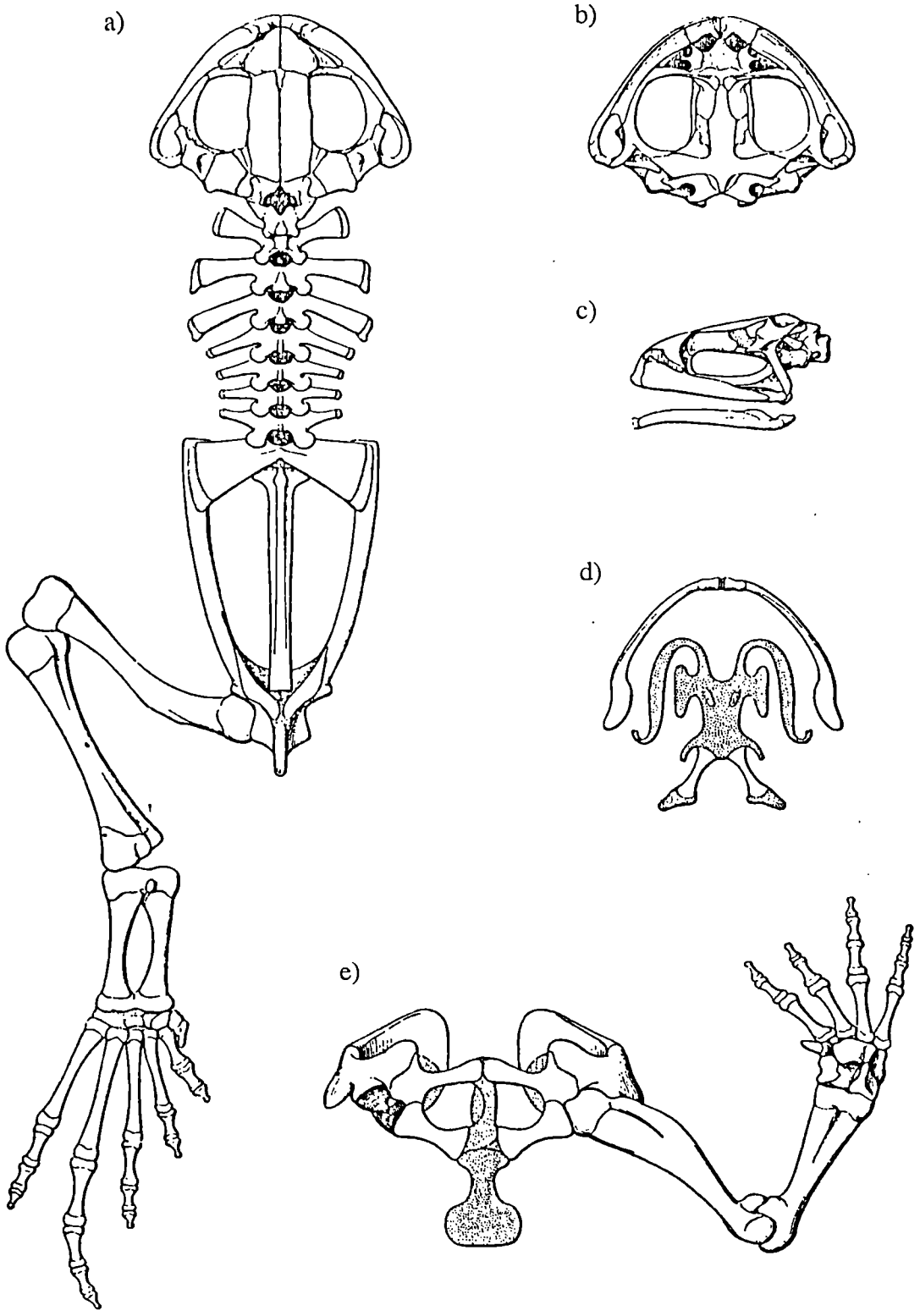


Figure 5.18 : Typical anuran skeleton (*B. bufo*): a) cranium, vertebral column, pelvic girdle and left hindlimb in dorsal view; b) cranium in ventral view; c) cranium and mandible in left lateral view; d) mandibles and hyoidal system in ventral view; e) pectoral girdle and left forelimb in ventral view (after Boulenger, 1897-8).

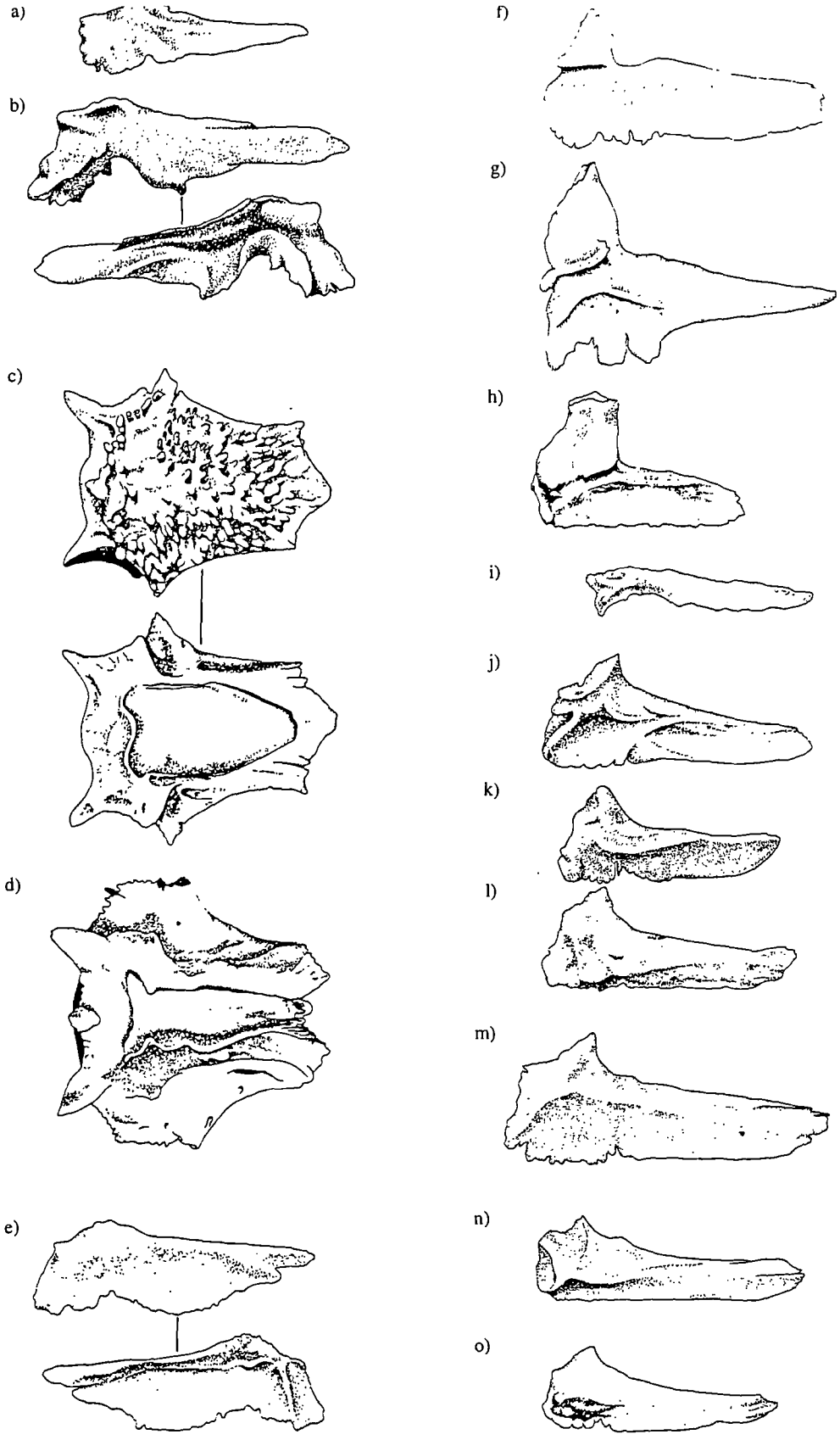


Figure 5.19 : Left frontoparietal (a, d, f-o - dorsal view; b-c, e - dorsal and ventral views) of: a) *B. variegata*; b) *A. obstetricans*; c) *P. fuscus*; d) *P. cultripes*; e) *P. punctatus*; f) *B. bufo*; g) *B. calamita*; h) *B. viridis*; i) *H. arobrea*; j) *R. temporaria*; k) *R. arvalis arvalis*; l) *R. arvalis wolterstorfii*; m) *R. dalmatina*; n) *R. ridibunda*; o) *R. lessonae* (after Böhme, 1977).

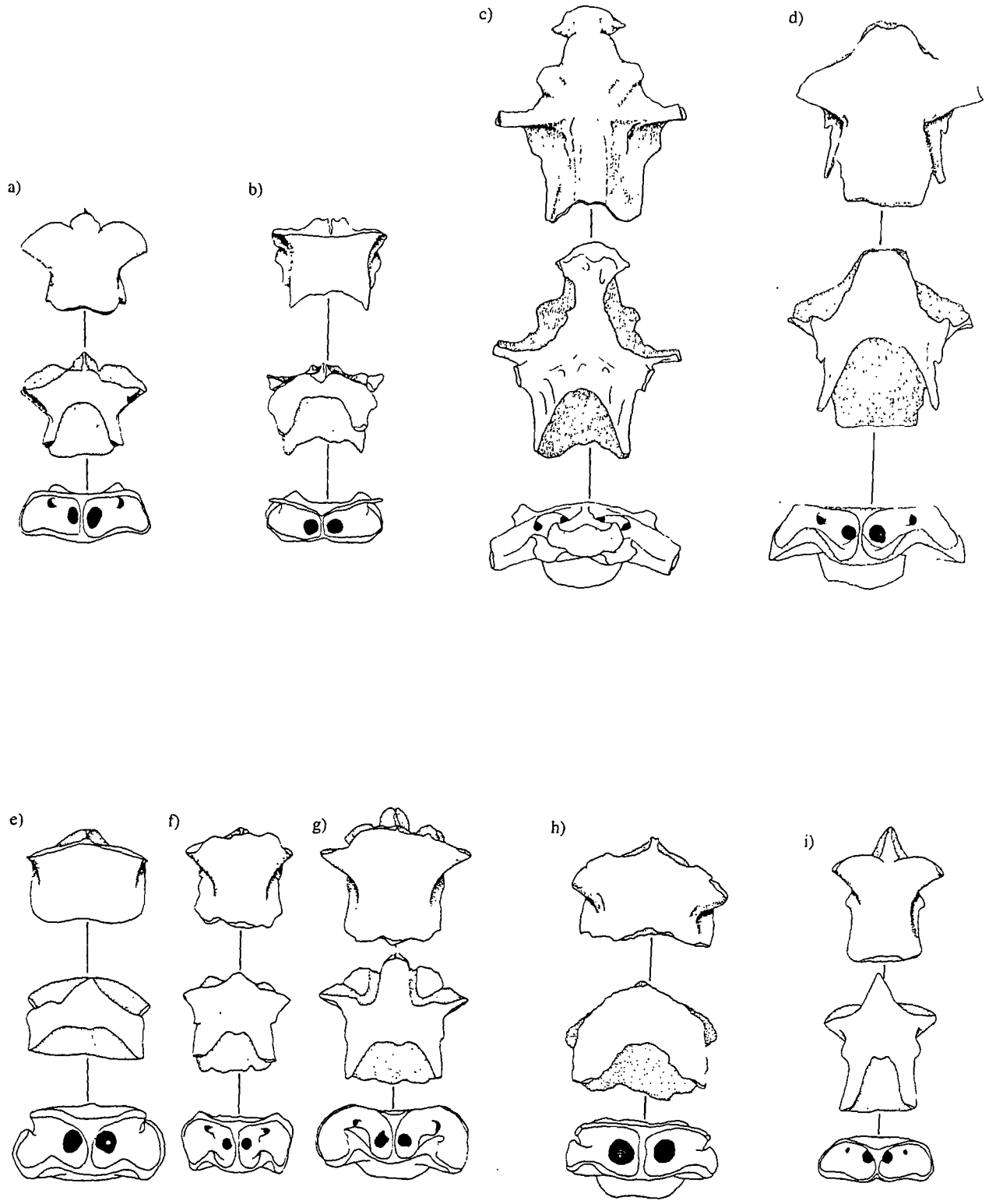


Figure 5.20: Sphenethmoid (ventral, dorsal and anterior views) of: a) *B. bombina*; b) *A. obstetricans*; c) *P. fuscus*; d) *P. punctatus*; e) *B. bufo*; f) *B. calamita*; g) *B. viridis*; h) *H. arborea*; i) *R. arvalis arvalis* (after Böhme, 1977).

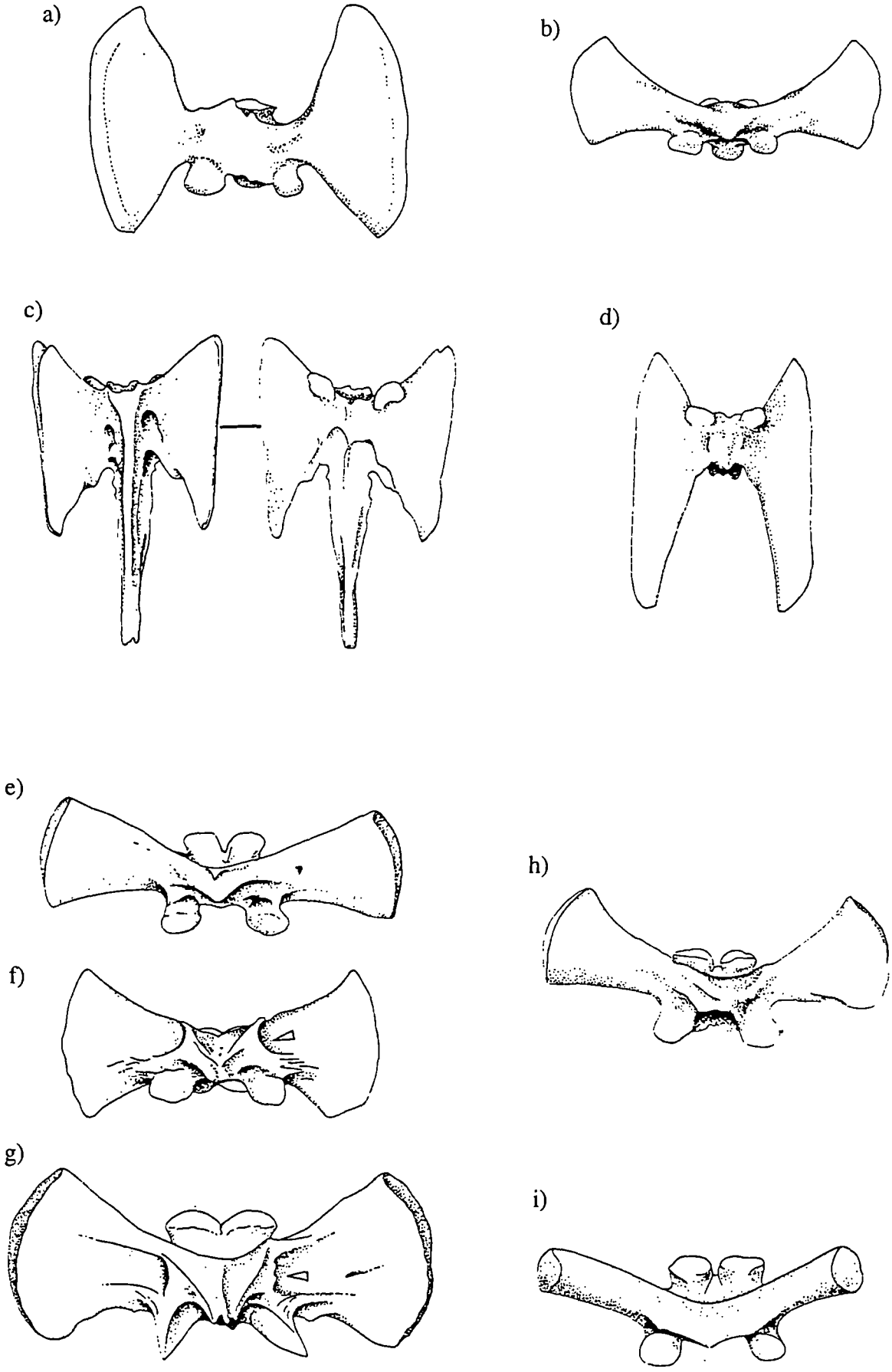
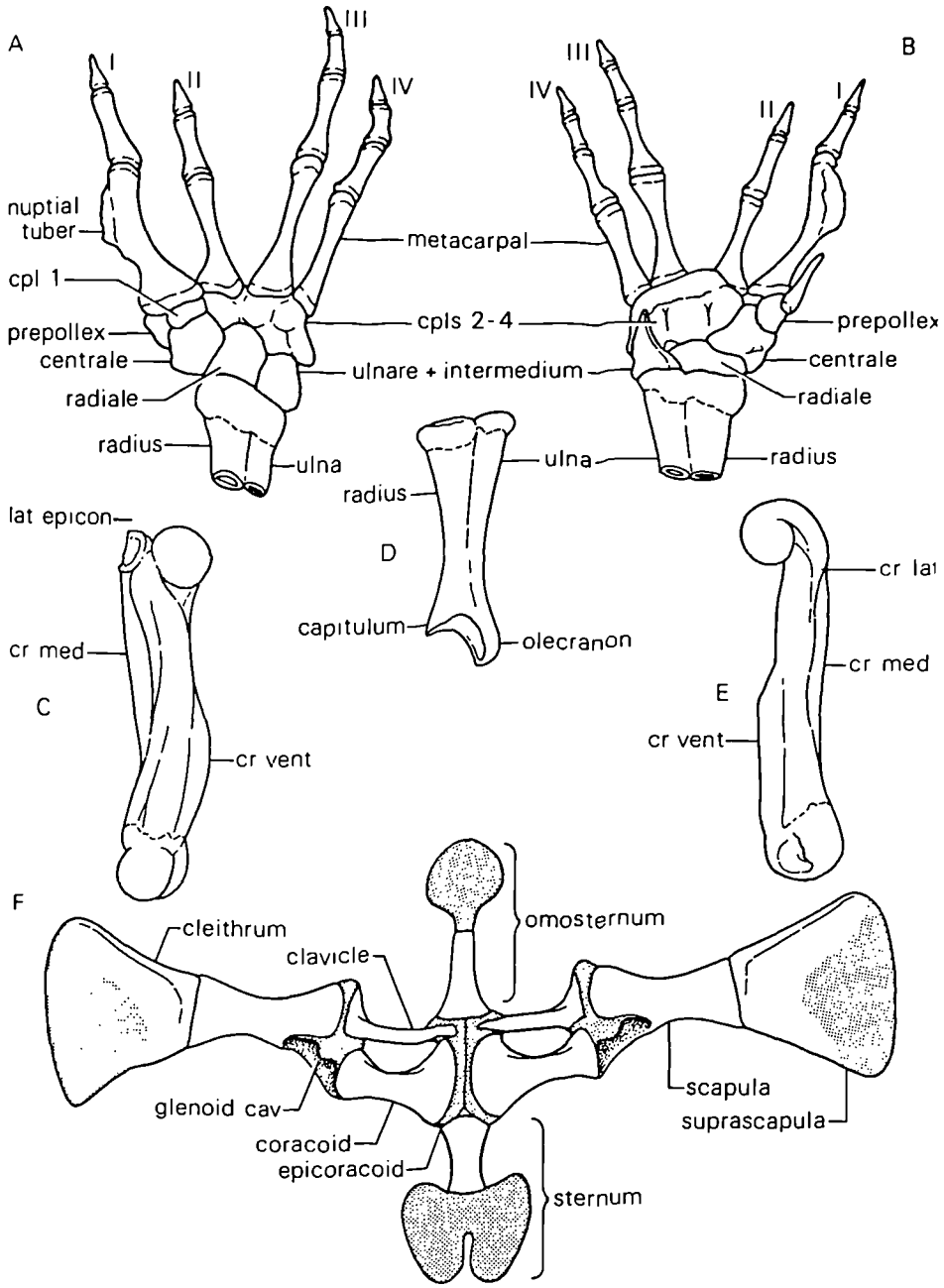


Figure 5.21 : Sacrum (a-b, d-i - dorsal view; c - ventral and dorsal views) of: a) *B. bombina*; b) *A. obstetricans*; c) *P. fuscus*; d) *P. punctatus*; e) *B. bufo*; f) *B. calamita*; g) *B. viridis*; h) *H. arborea*; i) *R. dalmatina* (after Böhme, 1977).



Anterior appendicular skeleton of *Rana esculenta* redrawn from Gaupp (1896). **A.** Dorsum of right hand. **B.** Venter of hand. **C.** Medial view of right humerus. **D.** Dorsal view of right radioulna. **E.** Lateral view of right humerus. **F.** Pectoral girdle in ventral view with scapula and suprascapula deflected ventrally into abdominal plane. Stippled areas are cartilaginous. Abbreviations: cav = cavity; cpl(s) = carpal(s); cr lat = crista lateralis; cr med = crista medialis; cr vent = crista ventralis; lat epicon = lateral epicondyle; tuber = tuberosity.

Figure 5.22: Right forelimb and pectoral girdle of *R. esculenta* (after Duellman and Trueb, 1986).

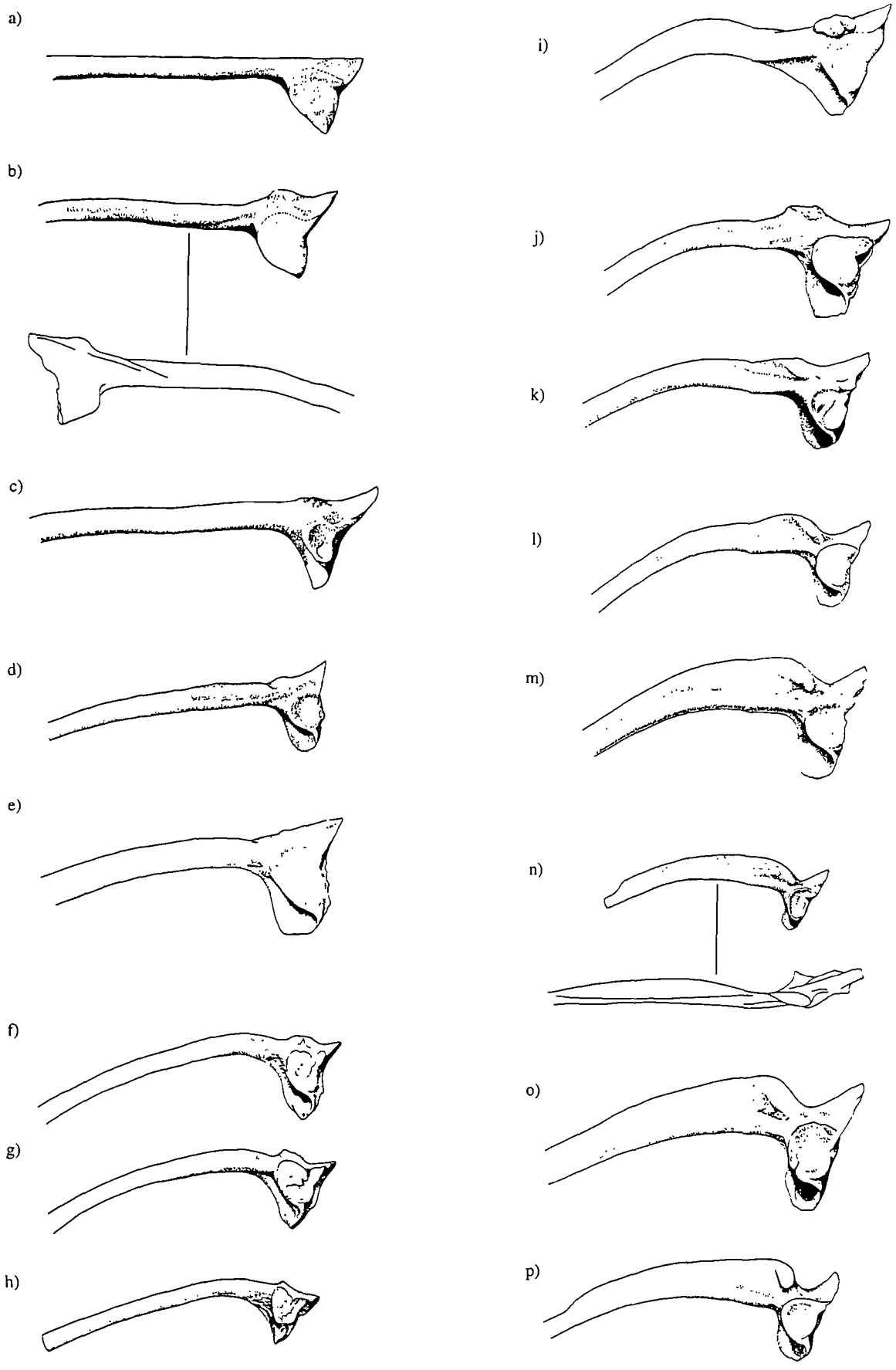


Figure 5.23 : Left ilium (a, c-m, o-p - lateral view; b - lateral and medial views; n - lateral and dorsal views) of: a) *B. variegata*; b) *B. bombina*; c) *A. obstetricans*; d) *P. fuscus*; e) *P. punctatus*; f) *B. bufo*; g) *B. calamita*; h) *B. viridis*; i) *H. arborea*; j) *R. temporaria*; k) *R. temporaria*; l) *R. arvalis arvalis*; m) *R. arvalis wolterstorfii*; n) *R. dalmatina*; o) *R. ridibunda*; p) *R. lessonae* (after Böhme, 1977).

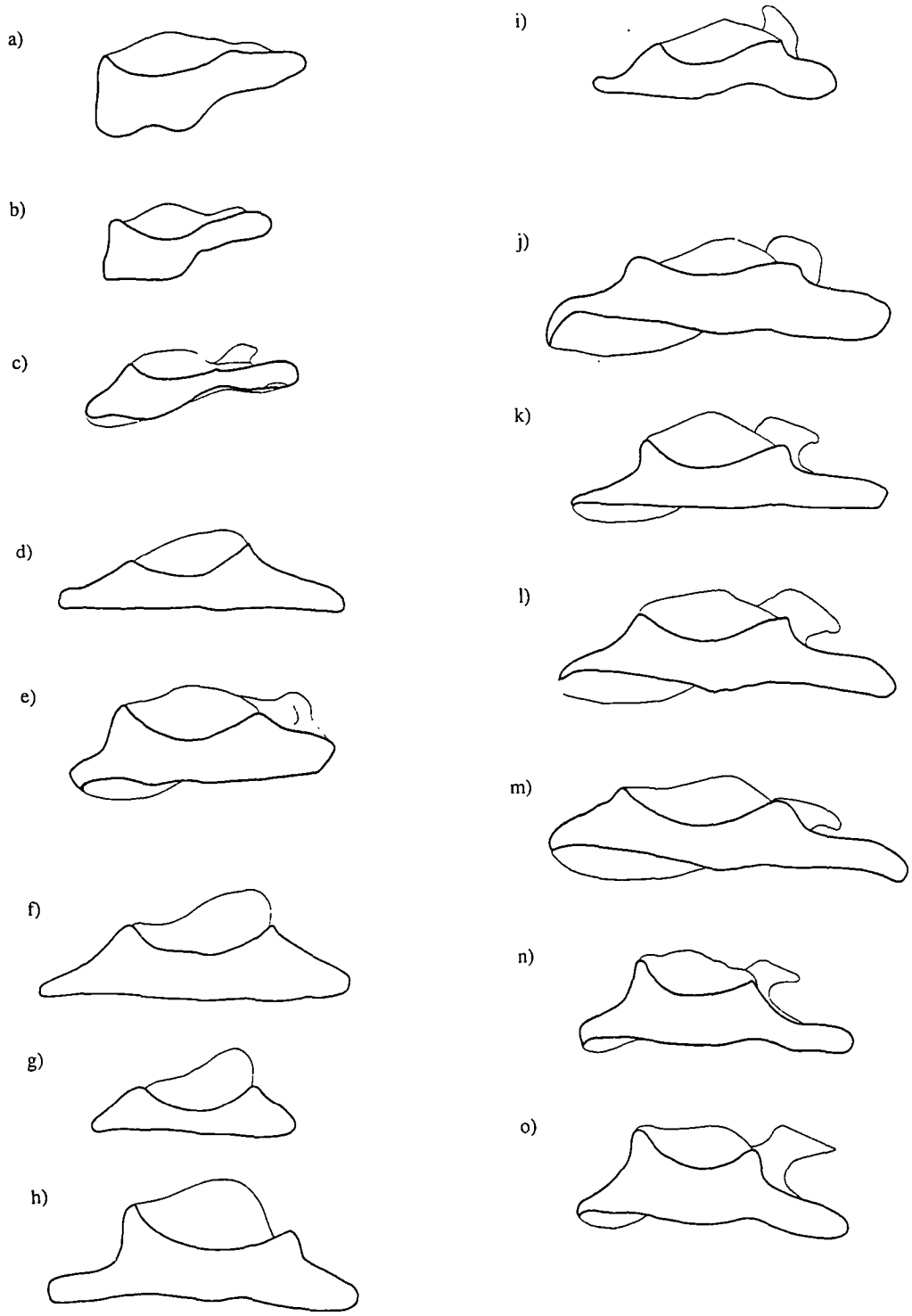
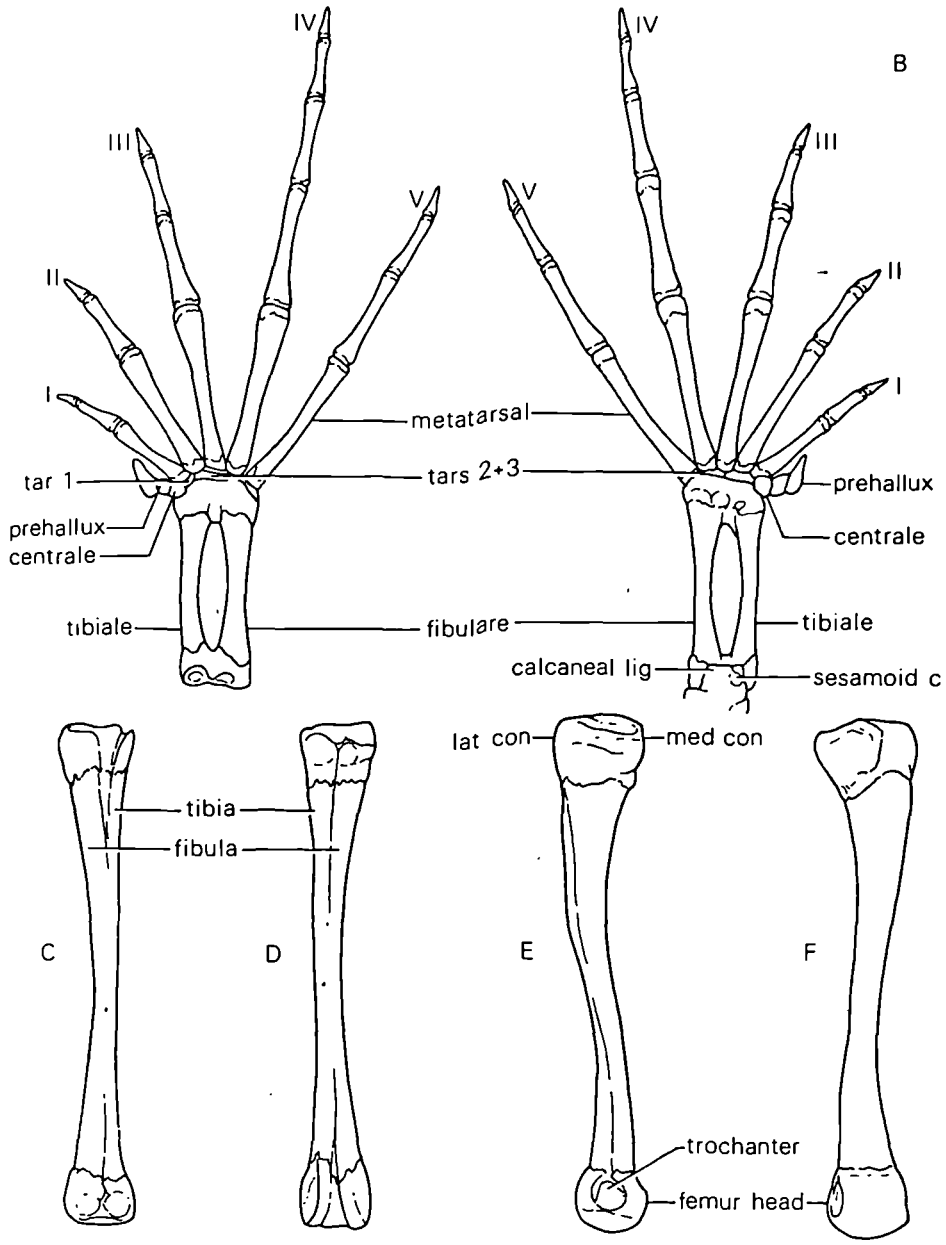


Figure 5.24: Junctura ilioischiadica of left ilium of: a) *B. variegata*; b) *B. bombina*; c) *A. obstetricans*; d) *P. fuscus*; e) *P. punctatus*; f) *B. bufo*; g) *B. calamita*; h) *B. viridis*; i) *H. arborea*; j) *R. temporaria*; k) *R. arvalis arvalis*; l) *R. arvalis wolterstorfii*; m) *R. dalmatina*; n) *R. ridibunda*; o) *R. lessonae* (after Böhme, 1977).



Posterior extremity of *Rana esculenta*, redrawn from Gaupp (1896). **A.** Dorsum of right foot. **B.** Venter of foot. **C.** Right tibiafibula in ventral view and **D.** dorsal view. **E.** Right femur in lateral view and **F.** medial view. Abbreviations: c = cartilage; lat con = lateral condyle; lig = ligament; med con = medial condyle; tar(s) = tarsal(s).

Figure 5.25: Hindlimb of *R. esculenta* (after Duellman and Trueb, 1986).

5.4 Discoglossidae

(*Bombina bombina, Bombina variegata, Alytes obstetricans*)

In the absence of comparative specimens for this family, the descriptions by Boulenger (1897-8) are very useful. In many ways, Bombina and *Alytes* are osteologically distinct from other genera. This is clear from illustrations by Böhme (1977) and Madej (1965). To date, there are no fossil records of the group in Britain, though it is a theoretical possibility that such remains will be found.

The most useful descriptions of *Bombina* osteological character, with diagnostic information, were given by Sanchiz and Mlynarski (1979). These authors detailed fossil material from the Polish Neogene. They concluded that *Bombina* is osteologically very distinct from other anurans, but that the two species are very similar indeed to one another. Madej (1965) and Hodrová (1981) also gave useful diagnostic information which is considered below.

No *Bombina or Alytes* specimens have been obtained during the current project. Two specimens of *B. bombina* and two *B. variegata* have been examined briefly at the Department of Zoology of the NHM, and were described originally by Boulenger (1897-8). These are: *B. bombina* (Ref nos. '1915.9.15.12/87.12.6.3' and 'Lataste coll. 1920.1.20.665 p.448'); *B. variegata* ('Lataste 1920.1.20.741. p.448' and 'RR .1937.7.29.52. 43a'). Unfortunately, the specimens are articulated and still possess some connective tissues, making their study difficult. This situation highlights the general lack of amphibian and reptile comparative material in British collections, which has probably been instrumental in the paucity of work in this field. Several specimens of *B. bombina, B. variegata* and *A. obstetricans* were briefly studied at the MNCN (Madrid). There is little description of this species in the literature. Rage (1974) described some French Quaternary fossils, and illustrated a few elements. Osteological nomenclature follows that of Böhme (1977) and Hodrová (1981).

CRANIAL BONES

Frontoparietals

The frontoparietals of *B. variegata* and *A. obstetricans* were illustrated by Böhme (1977), and are shown in Figure 5.19a. The frontoparietals of *Bombina* have an irregular saw-toothed medial edge to the pars parietalis, very similar in appearance to *B. calamita*. In *Bombina*, however, they do not fuse to the prootics, and are considerably smaller than *B. calamita*.

VERTEBRAE

Discoglossid vertebrae have not been studied during this project. However, Madej (1965) who studied large numbers (over 1300 specimens) of both *Bombina* species, comparatively, was unable to find diagnostic differences in the vertebral column. Sanchiz and Mlynarski (1979) and Hodrová (1981) reached the same conclusion. Madej (1965) described the vertebral series, with good

quality illustrations. Unfortunately, it is not clear if separation of *Bombina* and *Alytes* is simple, using vertebrae. The trunk vertebrae are small and almost cylindrical. In *Bombina*, the second, third and fourth vertebrae have short transverse processes to which ribs are weakly attached. Together, these are comparable to the longer transverse processes of other anuran genera. In fossil material, these ribs tend to detach, leaving very short transverse processes, e.g. in specimens illustrated by Sanchiz and Mlynarski (1979). The posterior trunk vertebrae appear to be readily diagnostic by their needle-like transverse processes, which are directed almost anteriorly. *A. obstetricans* also has very very similarly structured trunk vertebrae (Rage, 1974)

The vertebral column of *Bombina* can exhibit an extraordinarily high degree of variation (see Figure 5.26). Madej (1965) examined over 1,300 *Bombina* specimens, and found variation in around 10% of these. The atlas is of variable shape, as is the number of vertebrae. Most striking was the degree of assymmetry in the shape of the sacrum and the urostyle. Madej (1965) illustrated this region in twenty-five specimens. In some cases, an extra vertebra was formed from the anterior part of the urostyle. The sacrum normally possesses widely flared diapophyses, but some specimens had only one diapophysis, and the adjacent urostyle possessed 'the other' missing one (see Figure 5.26).

Sacrum

This bone is easily recognised in *Bombina*, as it has only one posterior condyle for articulation with the urostyle. There are also a pair of very widely flared diapophyses, the posterior tips of which extend much further than the anterior tips (Boulenger, 1897-8; Madej, 1965). See Figure 5.26 for *B. bombina*. In *A. obstetricans*, the sacrum has paired condyles and its diapophyses are not as widely flared, but still much more so than in *B. calamita*, and with the posterior tips extending further than the anterior tips.

Urostyle

The urostyle in *A. obstetricans* has a pair of short diapophyses, curved posteriorly. In *Bombina*, there is a pair of slender, posteriorly directed transverse processes. *Bombina* has only one cotyle for articulation with the sacrum, but *A. obstetricans* has two as in other genera (Boulenger, 1897-8).

PECTORAL GIRDLE

Scapula

This element is characteristically shortened, as it is partly cartilaginous. It is similar only to *Pelodytes*, but the acromion apophysis does not protrude in the same way (Rage, 1974).

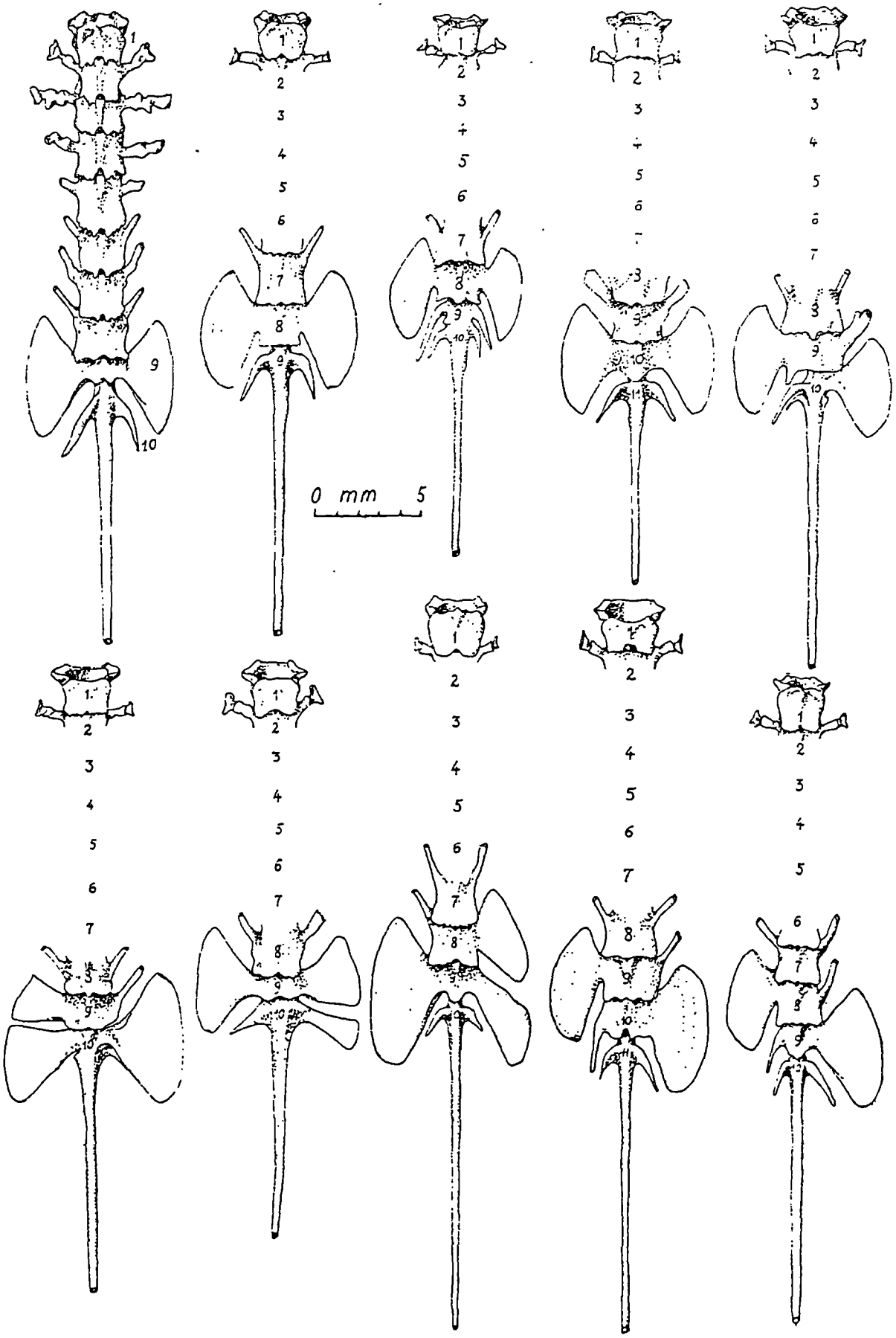


Figure 5.26 Variation in the vertebral morphology of ten specimens of *B. bombina* (after Madej, 1965).

PELVIC GIRDLE

Ilium

Böhme (1977) noted that the discoglossids, as a group, could be separated from all other European anurans, using the ilium. When viewing it by the junctura ilioischiadica, its pars ascendens is clearly much thinner than the rest of the corpus. He also noted that the ilium lacks a vexillum, in both *Bombina* and *Alytes*, but a tuber superior is developed on the corpus, above the acetabulum. This is strong in *Alytes*, but weak in *Bombina* and allows the separation of these genera. The corpus ends abruptly at its ventral edge, which is shouldered squarely, and lacks any real pars descendens (Böhme, 1977; Sanchiz and Mlynarski, 1979).

Though separation of *Alytes* and *Bombina* is possible, specific determination in *Bombina* is difficult. It appears that there is a 'typical' morphology for each species, but that transitional forms also exist. Detailed descriptions of *Bombina* ilia were given by Sanchiz and Mlynarski (1979) and Hodrová (1981). The latter author described the tuber superior in recent specimens as rather small, but in Late Pliocene fossil specimens, he found a range of variation from nearly imperceptible to highly prominent. Böhme (1977) found the tuber superior to be undiagnostic Hodrová (1981) was also unable to distinguish between *B. bombina* and *variegata* using the tuber superior alone, but inferred that a wide range of tuber superior size, seen in a fossil assemblage, would be an indicator of the presence of both species. Sanchiz and Mlynarski (1979) found that the tuber was higher in *B. bombina*, but more swollen and laterally-protuberant in *B. variegata*. From the current author's brief examination, the ilial tuber in *Bombina* seems to consist of a long ridge, with a higher tuber superimposed on it. The terminology of an ilial prominence and its ilial protuberance, used by Chantell (1964) for hylids, is equally appropriate in the description of *Bombina* ilia. The ilia of the NHM *B. bombina* seen had similar tubers, though one was better developed than the other. The smaller specimen had a long, straight, low ridge, with a higher bump mid-way along. The larger specimen had a stronger tuber, which was well-rounded and symmetrical, and of a similar size in relation to the corpus as in *Bufo*. Its sides were relatively steep, and the tuber prominent. Of the two *B. variegata* seen, one had a very low, long, poorly-developed tuber. The other had a fairly high, bulbous tuber, but with gently sloping flanks. Ontogenetic maturity may have some effect on the strength of the tuber, as it does in *B. calamita*.

Sanchiz and Mlynarski (1979) found that a depression, known as the preacetabular fossa, is only present in *B. bombina*. However, Hodrová (1981) considered that this feature could not be quantitatively defined and was not useful in diagnosis. The shape of the junctura ilioischiadica was found by both of the above authors to be a reliably diagnostic feature. The medial side of the junctura is more angular in *B. bombina*, but more sinuous in *B. variegata*. Hodrová (1981) was less certain of its use in fossil material, however, as intermediate forms were observed, and only 'typical' forms could be diagnosed.

Hodrová (1981) found that in *B. bombina*, there is always a bulbous cranially-directed tubercle on the medial side of the corpus (visible from the junctura ilioischiadica), whereas in *B.*

variegata, this is sometimes absent. The absence of this feature should therefore be diagnostic of *B. variegata*, but Böhme (1977) found that it is present in some populations of *B. variegata*. The *B. bombina* seen by the current author had a strong hump towards the anteroventral corner of the medial corpus face. Sanchiz and Mlynarski (1979) concluded that no single character is unequivocally diagnostic, but that their combination can allow specific differentiation without doubt.

APPENDICULAR SKELETON

Tibiofibulae and humeri

The tibiofibulae of *Bombina* are distinct in that the tibia and fibula are of unequal size, one being around four-fifths of the diameter of the other. This obvious assymmetry may be useful in diagnosis of discoglossids.

Rage (1974) noted that the distal condyle of the humerus in discoglossids is not in line with the diaphysis, being more exteriorly placed. It appears that this is most accentuated in *Bombina*. *A. obstetricans* also appears to have distinctively broader, shorter humeri than any other genera. The fossa cubitalis ventralis, above the distal condyle, is also shallow or absent in the Discoglossidae (Rage, 1974). The humeri of *Bombina* are very straight, with wide lateral and medial cristata in males, superficially similar to *Rana*. There is a strong crista ventralis, projecting as a prominent blade from the upper part of the humeral shaft. Its outline is variable between rounded and angular, from the specimens seen. Sanchiz and Mlynarski (1979) could find no diagnostic differences in the humeri and tibiofibulae of *B. bombina* and *B. variegata*.

5.5 Pelobatidae

(*Pelobates cultripes, Pelobates fuscus*)

No modern specimens have been obtained for study, but fortunately these are skeletally distinctive species. Two specimens of each species were studied at the MNCN (Ref. nos. MNCN 18035, 18045, 18089 and 18090). Böhme (1977) provided good illustrations of several skeletal elements for *Pelobates*. Some of these are without doubt sufficient for diagnosis and are illustrated well by the above author. Separation to species within the genus *Pelobates* is possible due to the very distinctive nature of certain cranial elements (Böhme, 1977). Bolkay (1933) provided satisfactory illustratrations of some cranial elements for *P. cultripes* and *fuscus*. No other descriptions have been found of recent *Pelobates*, but fossil material from Central European locations is well known (e.g. Hodrová, 1985).

Fossil material of *Pelobates* from Gorham's Cave, Gibraltar, has also been examined at the NHM and agrees with descriptions in the literature. Osteological nomenclatue follows that of Böhme (1977).

CRANIAL BONES

Frontoparietals

These are fused together into a single bony plate which is highly ossified and sculptured. This and other dermal bones of the cranium are highly distinctive due to their rugose surface patterning, and should not be confused with any other genus. Böhme (1977) illustrated the frontoparietals of *P. fuscus* and *cultripes* (Figure 5.19c,d), and the drawings are sufficient for specific diagnosis. Bolkay (1933) also illustrated these elements. Given that these two species have different head shapes, the differences in cranial osteology are not surprising. The narrower, more domed head of *P. fuscus* is reflected in a narrower frontoparietal, each side with an acute processus prooticalis. The ventral side has a wide endocast (braincase mould). Contrastingly, *P. cultripes* has a wider head, without a prominent parietal dome (Morrison, 1994) and a correspondingly wider frontoparietal, though with a narrower endocast. It also has a clearly indented anterior margin, and instead of acute lateral processes, each side has a wide, straight margin connecting with the prootics. This could be referred to as the margo prooticalis, rather than the processus prooticalis. These differences are also reflected in the shape of the prootics. These two species could be separated using other cranial elements, but these have not been studied in enough detail to give full descriptions here. Hodrová (1985) also compared frontoparietals of recent *P. fuscus* with *P. syriacus balcanicus* (an eastern species). The illustrations are good, and show that *P. fuscus* has a relatively flat frontoparietal, compared to the very domed *P. s. balcanicus*.

Squamosals

Bolkay (1933) illustrated a squamosal of *P. fuscus*, showing the ornamented surface which is

diagnostic of the genus. This ornamentation is present on all dermal bones in the cranium.

VERTEBRAE

The trunk vertebrae of *Pelobates* are similar to those of *Pelodytes, Bombina* and *Alytes*. The third vertebra has wide, assymmetrical transverse processes, with small accessory spines on their posterior edge. The neural spine forms a posteriorly directed, pointed crest. The fifth has short, sharp, anteriorly directed transverse processes, positioned beneath the prezygapophyses. Its neural spine forms a sharp ridge and is produced posteriorly. The seventh has no transverse processes and its neural spine is not produced. The anterior neural arch has a small V-shaped notch in it, reaching posteriorly further than the prezygapophyses, except in the sixth, seventh and eight vertebrae. There are no obvious differences between the two species.

Sacrum and Urostyle

From Boulenger's (1897-8) illustrations, the sacrum of *Pelobates* is very distinctive. The urostyle is fused to it, and extends posteriorly as a tapered rod. The diapophyses of the sacrum are very widely flared, as in *Bombina* and *Pelodytes*. Though *Bombina* can have a fused urostyle (Madej, 1965), the diapophyses in *Pelobates* are distinctive as they are equally extensive anteriorly and posteriorly, and have a very symmetrical shape.

PELVIC GIRDLE

Ilium

The ilium of *Pelobates* is like that of *Pelodytes* (discussed below) in that it lacks the vexillum and tuber superior, found either singly or together in the other European anuran genera. It pars descendens is much thinner than in *Pelodytes* which has superficially similar ilia (compare Figures 5.24d/e). Also, where the ala joins the corpus, an oblique groove passes across the dorsal surface, posterolaterally to anteromedially. Holman (1992a) gave an identification of *P. fuscus* using ilia, but had not seen *P. cultripes* type material. Therefore this identification should be considered uncertain, and may represent either species. From the few specimens seen, there appear to be subtle differences between ilia of the two species. *P. fuscus* has a slightly wider and more angular pars descendens, and the proximal portion of the ala is flatter dorsolaterally. In *P. cultripes* the outline of the pars descendens is more rounded and the ala is more cylindrical proximally. There may be light sexual dimorphism in the ilia of these species, with a slightly greater arch in the profile of the ala of the two female specimens (MNCN 18035, 18089), when viewed dorsally. If this is consistent, it would imply a slightly wider pelvic region in females.

5.6 Pelodytidae

(Pelodytes punctatus)

This species is the only European representative of the family. Böhme (1977) figured several skeletal elements and gave very brief diagnostic notes. Rage (1974) illustrated several elements from French Quaternary deposits, and Böttcher (1994) detailed remains from the German Quaternary. The German descriptions have not been translated, but the author appears to have given good diagnostic descriptions for *P. punctatus* and two other species: *P. arevacus* and *P. caucasicus*. Holman (1991) recorded *P. punctatus* from Westbury-sub-Mendip and illustrated three ilia. The only detailed work in English was that of Ridewood (1897), on the hyobranchial apparatus, including a description of the hyoidal cornua.

No specimens have been obtained for the current study, but a few specimens were briefly studied at the MNCN. Thus, only brief osteological descriptions and diagnostic criteria are given. Osteological nomenclature follows that of Böhme (1977), and Rage (1974) where appropriate.

CRANIAL BONES

Frontoparietals

These are fairly distinctive in shape (see Figure 5.19e), but are not dissimilar to those of *A. obstetricans*. This could be problematic in imperfect fossil specimens. However, the ventral surface exhibits a ridge below the lateral margin and traversing the parietal portion of the bone. It would appear that it is possible in this case to use Böhme's (1977) drawings quite safely for diagnosis.

Sphenethmoid

This is widely flared anteriorly and, from drawings (Böhme, 1977; Böttcher, 1994), is apparently diagnostic (Figure 5.20d).

VERTEBRAE

The trunk vertebrae appear to be similar to discoglossid and pelobatid vertebrae, in drawings given by Rage (1974), with sharply anteriorly directed transverse processes in the posterior vertebrae.

Sacrum

This has very widely flared diapophyses, even more so than in *Bombina*, and the posterior tips extend further than the anterior tips. There are also two articular condyles as opposed to one in *Bombina* (Boulenger, 1897-8).

Urostyle

This is slender and has no diapophyses, thus distinguishing it from discoglossids.

PECTORAL GIRDLE

Scapula

The scapulae are very short and truncated distally, and very similar in shape to the discoglossids. However, the acromion apophysis forms a protuberance which is not present in the Discoglossidae (Rage, 1974).

PELVIC GIRDLE

Ilium

The ilium in *P. punctatus* has no vexillum or tuber (Böhme, 1977). The corpus apparently has a very thick pars ascendens, seen in posterior view from the junctura ilioischiadica, with a medially curved pars descendens (see Figure 5.24e). It seems likely that these features collectively distinguish *Pelodytes* from all other European anuran genera. Böttcher (1994) illustrated several ilia, comparing them with those identified from Westbury Cave (Holman, 1993a).

5.7 Bufonidae

(*Bufo bufo*, *Bufo calamita*, *Bufo viridis*)

Bolkay (1917) gave some illustrations of European *Bufo* bones, but these are limited in their usefulness. Böhme (1977) addressed the comparative osteology of the European bufonids, and briefly described the ilium as well as giving notes on the sacrum, sphenethmoid and frontoparietals. As the sacrum and frontoparietals are very distinctive for *Bufo* species, the drawings provided are useful. Sanchiz (1977) gave a useful account of Spanish Tertiary bufonids, including comparative osteological descriptions of *B. bufo* and *B. calamita*.

Of the three European species of bufonid toad, *B. calamita* and *B. bufo* are present in the British Isles today, and both have been recorded as fossils. The osteological literature has already illustrated some of the features allowing distinction between these two species, but there is still potential for misidentification. The form of the ilium is most commonly used in differentiation. Other skeletal elements have received little or no attention, though a consideration of these ought to be included, both for completeness and to maximise the potential usefulness of any sub-fossil material. Holman (1989b; 1992a) has described characters for the specific identification of *Bufo* ilia, and has made several records of fossil *B. calamita* based on these criteria. In fact, the ilium of *Bufo* exhibits considerable intraspecific variation, and the characters described by Holman (1989b; 1992a) are insufficient. Unfortunately, of the cranial elements which are identifiable to species, most are found relatively infrequently as fossils.

Appendix 1 contains a list of the individual specimens studied, with all known details. Where particular specimens are referred to in the text, the respective reference numbers are given. Osteological nomenclature follows that of Böhme (1977), Gaupp (1896) and Ecker (1889).

CRANIAL BONES

Frontoparietals

The frontoparietals, as noted by Böhme (1977), are morphologically distinct in *Bufo* between species. In *B. bufo*, the frontoparietal is subrectangular, with a straight medial edge. This is slightly serrated along its posterior portion (pars parietalis). The anterior portion (pars frontalis) ends as an oblique edge. The lateral side of the pars parietalis is borded by a deep groove (fossa prooticalis), separating it from the triangular extension of the processus prooticalis. In *B. calamita*, the frontoparietal is somewhat triangular in shape, with a saw-toothed medial edge, tapering to a point at its anterior end. The pars parietalis is furnished with a pronounced ridge and associated nodules, which could be labelled the crista parietalis (equivalent to the lineae of Böhme, 1977). This crista overhangs a much more deeply-excavated fossa than in *B. bufo*, and is opposed by a similarly strong L-shaped ridge (crista prooticalis) bordering the processus prooticalis. The frontoparietals of these two species can thus be easily separated, due to their distinctive shapes. The frontoparietal of *B. viridis* is similar in overall shape to *B. bufo*, but it is narrower and unlike

B. bufo it tapers towards its anterior end. The medial edge of its pars parietalis is slightly more serrated. The fossa prooticalis is intermediate in depth, and the cristae bordering it are fairly pronounced and more akin to those of *B. calamita*. This combination of characters makes distinction possible from either of the other two species.

Parasphenoid

This is not immediately distinguishable from *Rana* on the basis of shape alone. It is neatly cruciform, without its lateral lobes being constricted or flared distinctively. However, it is more strongly produced ventrally, with cruciform ridges sloping towards the parallel edges of each lobe. This produces a diamond-shaped raised area when viewed ventrally. The steepness of the slopes is greater than in *Rana*, and the abruptness of their descent from the small central star-shaped central plateau is distinctive. In *B. calamita*, the posterior part of the raised diamond is not as fully enclosed, but the anterior end is pinched and bordered by lateral indentations.

Maxillae

The paired maxillae, together with the small premaxillae, form the semi-circular edge of the upper jaw. They are toothless in *Bufo* unlike in *Rana* and other European genera. The dorsal edge is uneven, as in other genera, and is produced into two sharp lobes. In *B. calamita,* the uneven dorsal blade is noticeably higher than in *B. bufo,* which conversely has a relatively wider ventral (occlusal) blade.

Angulosplenials

The angulosplenial has a thinner cross-section in *Bufo* than in *Rana*. The coronoid process is also longer, more rounded, and extends further posteriorly than in *Rana*. The lateral sulcus is deeper than in *Rana*. The ventral edge of the angulosplenial expands laterally as a horizontal flange towards its posterior end. In *Bufo* the ridged dorsal margin of the lateral sulcus ends beneath the coronoid process. Here it expands into a wide horizontal flange which extends beneath the coronoid process to the posterior tip of the bone. In *Rana,* this horizontal flange only occurs posterior to the coronoid process. In *Bufo*, the narrow sulcus ends at the coronoid process and often has a small lateral crista at its upper edge.

In *B. calamita*, the angulosplenial is slightly more curved and shorter than in *B. bufo*. There are no obvious diagnostic features and as this can be a fairly variable bone, specific identification is likely to be difficult in many cases.

Dentaries

These have a roughly cylindrical form, with a slightly depressed dorsal surface. The Mentomeckelian cartilege is long and narrow, tapering to a fine point in complete specimens.

Quadratojugals

These small bones connect proximally with the lower end of the squamosals, and distally with posterior tips of the maxillae. The articular end is larger and more flared in *B. calamita* than in *B. bufo*. The anterior process is shorter than in *Rana*, and uneven in its outline, particularly in *B. calamita*.

Nasals

These are small, curved plates which protect the olfactory capsule. The nasals in *Bufo* are thicker and more robust than in *Rana*, perhaps being of greater importance to a more terrestrial genus. The posterior edge is also noticeably thickened in *Bufo*. Otherwise they are relatively featureless bones with no obvious diagnostic characters.

Squamosals

These are T-shaped bones, which connect dorsally with the prootics of the braincase. The dorsal end extends as two opposed processes, but their much sharper tips distinguish *Bufo* from *Rana*. *B. bufo* and *B. calamita* are easily separated using this element, though this may be of limited use for fossil specimens as the dorsal part of this bone is fairly delicate. In *B. bufo*, the dorsal end is expanded posteriorly into two sharp spines connected by a thin concave lamina. The posteromedial one is directed medially and extends furthest. In *B. calamita*, the posteromedial spine is not deflected medially, but lies in line with the anterior process. The posterolateral spine is greatly reduced and easily distinguished from *B. bufo*.

Pterygoids

These are tri-lobate, with their anterior end connecting with the posterior half of the maxillae. In *B. calamita*, the anterior process is longer than in *B. bufo*. It is also wider, with an angular medial edge, and more curved in *B. calamita* than in *B. bufo*.

Sphenethmoid

Several points are worthy of note, regarding the sphenethmoid. Figure 5.20 shows the range of form within the European anurans (after Böhme, 1977). It is fairly distinctive in *Bufo*, particularly in *B. bufo* where it is notably shorter. Some specimens have rounded notches in the anterolateral edges, but in others these notches are enclosed as rounded foramina. There is some evidence that this may be sex-specific, with females tending to have enclosed foramina and generally slightly longer sphenethmoids. Males show more variability, but the overall length of the sphenethmoid is usually shorter. *B. calamita* does not appear to have any form of notches or foramina in the anterolateral edges.

Columellae

The columellae are conical trumpet-shaped bones associated with the middle ear. The proximal end is wider than the delicately pointed distal end which connects with the tympanum (ear drum). The columellae are widely conical in *Bufo,* whereas in *Rana* they are more slender. In *B. calamita* they are more robust than in *B. bufo*, with a roughened outline and a fairly sharp ridge running along its length.

Hyoidal cornua

These are paired rods which support the hyoidal apparatus. The ends are flared more widely in *Bufo*, and their overall form is more robust. In *B. calamita*, each cornu is twisted more noticeably than in *B. bufo*, with a roughened outline giving it a crooked appearance.

VERTEBRAE

As with almost all anurans, the vertebral column consists of nine vertebrae (atlas, seven trunk vertebrae, sacrum). The sacrum articulates with the anterior tips of the ilia. A tenth vertebral element, the urostyle, articulates with the sacrum andextends posteriorly as a tapering rod between the ilia. The vertebrae of *Bufo* are often very similar to that of *Rana*, and both genera exhibit a large amount of variation in the vertebral column. This includes the common occurrence of various forms of pathogenic fusion and deformity. This has been noted by other authors (e.g. Böhme, 1982). It would seen that at least some, if not most, of this pathogeny results from congenital conditions, caused by abnormal development in early growth stages, perhaps due to genetic defects.

Atlas

The atlas tends to have a much wider posterior articulation (condyle) on the centrum. This is likely to be wider and has a more elongate section in *B. calamita* and *B. viridis* than in *B. bufo*. The dorsal relief reflects that of the other vertebrae, but as this bone is often shorter, it may not be clearly developed. In general, the dorsal surface is fairly flat, with a recess underlying a posterior flange. The neural spine is rudimentary, but may be raised as a triangular area, positioned at the posterior edge of the neural arch.

Trunk vertebrae

Within the column, the trunk vertebrae are variable in their relative proportions. The transverse processes tend to be higher and angled more dorsolaterally (perpendicular to one another in anterior view) in *Bufo* than in *Rana* (where they are closer to obtuse). The laminae are steeper, and the neural canal is often narrower than in *Rana.* This is best seen from anterior or posterior view. The dorsal morphology of the vertebrae is diagnostic also. In *Bufo* there is usually a pronounced neural spine, variable in height and often acute. A transverse ridge is present in *Bufo*, but it is usually deflected posteriorly so that it overhangs the posterior neural arch as a flange. Beneath the edge of

this, a recessed area is separated by a thin ridge, which is effectively a continuation of the neural spine. The dorsal surface of trunk vertebrae is much flatter than in *Rana*, as opposed to the general convexity in *Rana*. Some *Bufo* vertebrae may not have the sharp flange overlapping the posterior arch, but the overall flat dorsal surface, and sharp neural spine, should be diagnostic.

Separation to species is possible using trunk vertebrae. In *B. calamita,* the vertebrae are generally more compact, with a squarer overall shape. The centrum is usually narrower, and the closer-set zygapophyses clearly overlap the centrum when viewed from above. The zygapophyses are set further apart in *B. bufo* and tend not to overlap the centrum when viewed dorsally, though in the posterior trunk vertebrae some overlapping occurs. The anterior neural arch may also be indented in a V-shape (viewed dorsally) in *B. calamita*, but less so in *B. bufo*. The neural spine projects poteriorly into this notch.

The transverse processes are relatively shorter in *B. calamita* than in *B. bufo*. In the second, third and fourth vertebrae, they are proportionately thicker and more flared. The size and direction of the transverse processes can be used to ascertain which vertebra in the column is being dealt with. The seventh and eighth can be separated as the latter is the only amphicoelus vertebra. The shape of the articular facets is also of some diagnostic value. The shape of the cotyles and condyles is different for each vertebra in the column, but for each it tends to be consistently wider and more elongate in *B. calamita.*

The second vertebra (Figure 5.27a,c,e) has short, flat, flared transverse processes. The anterior cotyle is wider and more elongate in *B. calamita* and *B. viridis*, corresponding with the condyle of the atlas.

The third vertebra is distinctive and tends to have its neural spine flattened posteriorly in *Bufo* (see Figure 5.27b,d,f). This forms a rugose, roughly triangular area (contrasting, for example, with the tubular crest in *Rana* third vertebra). Its transverse processes are directed downwards, with their tips below the level of the centrum. This prevents the bone from lying flat, and when rested on a flat surface, the anterior end of the centrum will be elevated. As the processes are longer in *B. bufo*, the centrum is raised higher from the surface upon which it is resting. The proximal portion of the processes has a dorsal protuberance, which may be produced into a tuberous nodule or short spine. The tips of the processes are flattened and flared, more so in *B. calamita*, and tilted with the dorsal side facing anterodorsally. The angle of tilt is greater in *B. bufo*; the processes are flatter in *B. calamita*. Unfortunately, the single specimen of *B. viridis* studied has a pathogenically fused third and fourth vertebra, but appears bery similar to *B. calamita* otherwise.

The fourth vertebra has equally long processes but these are tilted slightly upwards. The anterior neural arch is produced anteriorly, forming angular lateral corners. The processes are altogether longer, straighter and narrower in *B. bufo.*

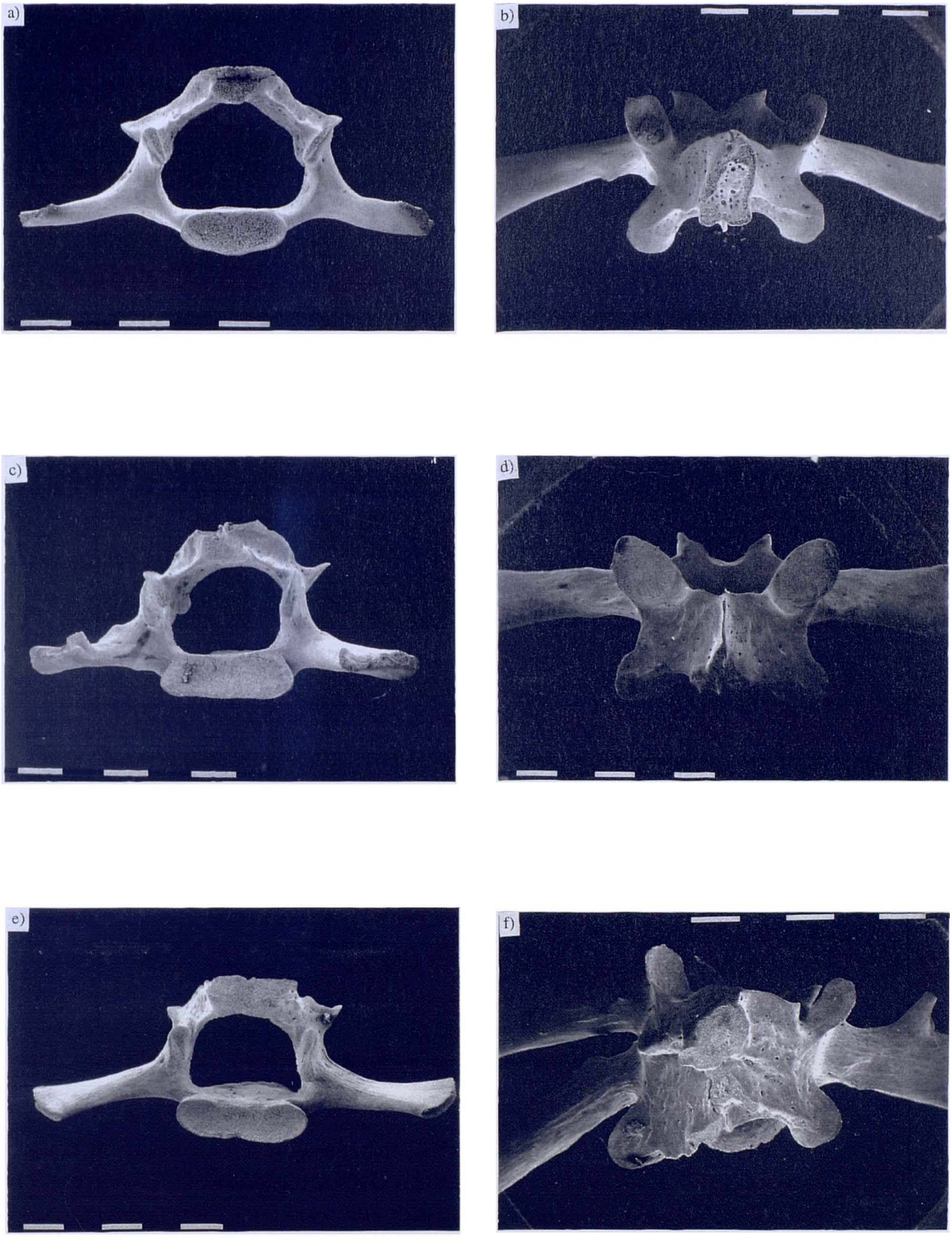


Figure 5.27 : Dorsal view of: a) second vertebra of *B. bufo* (CGO 1/10); b) third vertebra of *B. bufo* (CGO 1/7); c) second vertebra of *B. calamita* (CGO 17/1); d) third vertebra of *B. calamita* (CGO 17/7); e) second vertebra of *B. viridis* (CGO 29/1); f) pathologcal third/fourth vertebra of *B. viridis* (CGO 29/1).

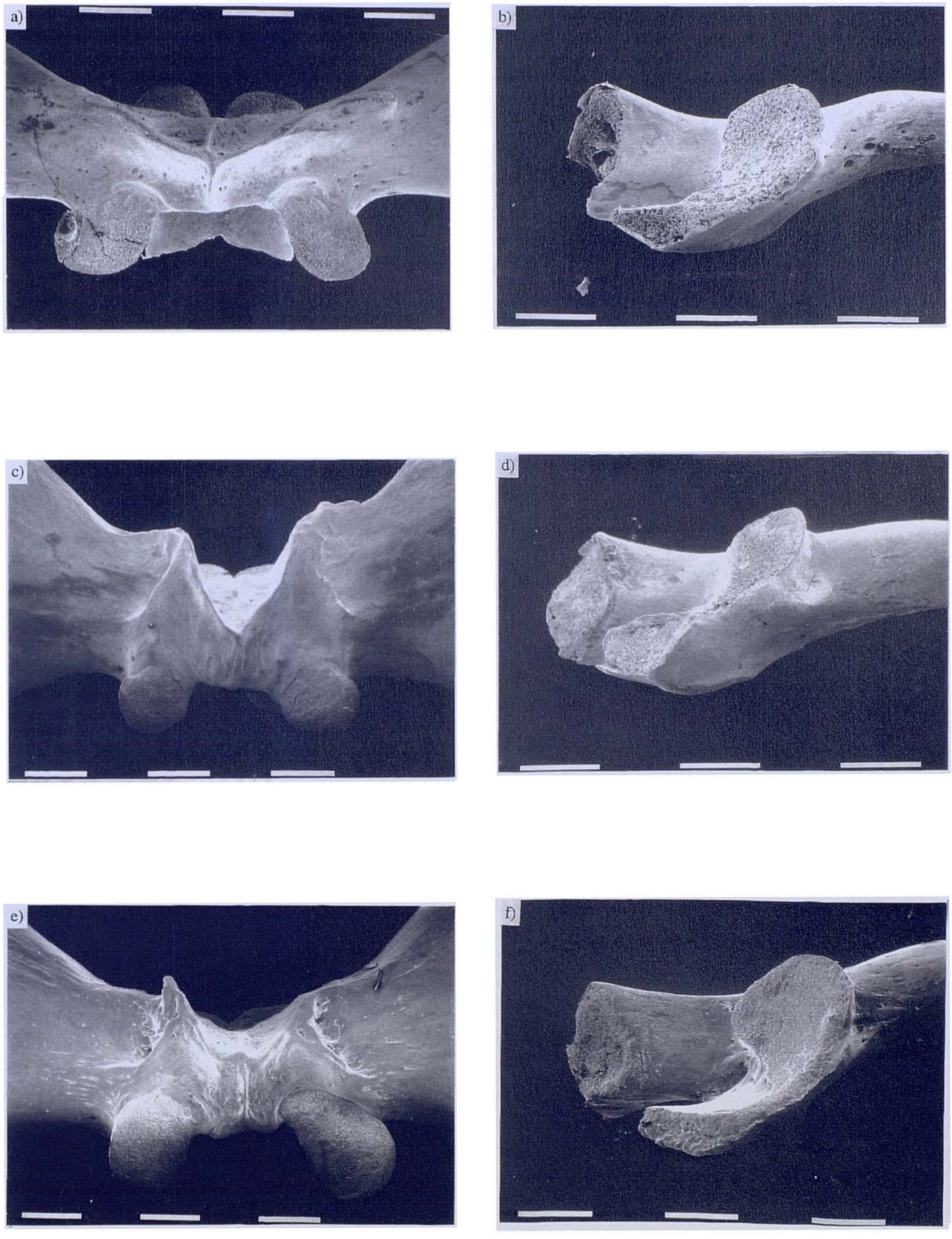


Figure 5.28:a) sacrum (dorsal view) of *B. bufo* (CGO 1/5); b) L. scapula (anterior view) of *B. bufo* (CGO 1/5); c) sacrum (dorsal view) of *B. calamita* (CGO 17/1); d) L. scapula (anterior view) of *B. calamita* (CGO 17/1); e) sacrum (dorsal view) of *B. viridis* (CGO 29/1); f) L. scapula (anterior view) of *B. viridis* (CGO 29/1).

Sacrum

The sacrum is very distinctive in *Bufo* (Figure 5.28a,c,e). It has a pair of lateral apophyses which are widely flared. This is much more pronounced in *B. calamita* and *B. viridis*. To confirm identification, the dorsal relief should be considered. This is particularly useful in damaged specimens, lacking intact lateral apophyses. In *B. bufo*, there is a cruciform relief, whereas in *B. calamita* there is a clear V-shaped relief, with the posterior neural arch produced into angular laminae. Iin *B. viridis*, these are produced into spines. In *B. viridis* there are also deep, crescentic dorsal fossae at the base of the lateral apophyses. In *B. calamita* there is a depressed area here, but no fossae.

Urostyle

This elongate rod is effectively a continuation of the vertebral column. Also known as the os coccygis, it has a well-developed dorsal blade which is equivalent to the neural spine of the vertebrae. Separation from the other European genera is easily done on the basis of shape and size. In *B.bufo*, the urostyle is not easily separated from that of brown frogs. *B. calamita* and *B. viridis* are more easily diagnosed because of their distinctly elliptical anterior cotyles, which connect with the correspondingly elliptical condyles of the sacrum. The neural spine is also lower in *B. calamita* and *B. viridis* than in *B. bufo*, and the urostyle is overall more robust and stockier in shape.

PECTORAL GIRDLE

Scapulae

The scapula in *Bufo* (Figure 5.28b,d,f) lacks the dorsomedial ridge found in *Rana*. Close to the glenoid articulation, a deep fossa is found in *B. calamita* and to a lesser extent in *B. viridis*, but not in *B. bufo*. Sometimes in *B. bufo* there is a small foramen in this position, but its size never approaches that of the fossa supraglenoideum in the other species.

Coracoids

These are cylindrical at their distal ends and flared at their proximal end where they articulate with each other. In *B. calamita* the proximal end is more widely flared and the posterior edge more concave as a result. The distal end articulates with the proximal end of the humerus and the scapula (Ecker, 1889). There is a large foramen on the distal articulation, bordered by a narrow area of articulation which connects with the curved processus coracoideus of the scapula. The relative shape, size and position of this foramen may be helpful in diagnosis.

Precoracoids

These are much more robust than the narrow needle-like precoracoids in *Rana*. In *B. bufo*, the medial tip is relatively narrow, but in *B. calamita* it is much wider and noticeably flared.

PELVIC GIRDLE

Ischium

This bone ossifies well, and is often preserved fossil, but useful diagnostic features have not been found. Its overall shape is semicircular, extending ventrally well below the acetabular margin. In *B. calamita* the postroventral corner is squarer than *B. bufo* in which it is more rounded.

Ilium

See Figures 5.29-5.32. The three species of *Bufo* considered here can be separated, using consistent morphological features of the ilium. Sanchiz (1977) and Nemec (1945) have, among others, dealt with the identification of *Bufo* ilia, though only the latter discussed this element in detail. Holman (1989b; 1992d) briefly discussed diagnostic criteria, but from the range of variation seen in both fossil and recent specimens, these characters should be refined. As noted previously (Nemec, 1945; Sanchiz, 1977; Holman, 1989b), the ilium of *B. viridis* has a large, deep preacetabular fossa which distinguishes it from *B. bufo* and *calamita*. This character alone allows firm and consistent diagnosis of *B. viridis*. The three characters given by Holman, for diagnosis of the other two species, are considered below, and additional criteria are discussed.

Tuber superior

Separation of *B. bufo* and *B. calamita* relies mainly on the form of the tuber superior. As has been noted (Holman, 1985; 1988; 1989b; 1992d; Holman & Stuart, 1991), the tuber is more triangular in outline and more pointed in *B. calamita* than in *B. bufo*. Vergnaud-Grazzini (1970) described it as more prominent and 'sculpted' in *B. calamita*. Hodrová (1985) described the tuber in *B. bufo* as having tubercles, referring to its irregular lateral surface. Holman (1989) considered the ilium of *Bufo* to be a reliably consistent element, but it actually has a very variable form in the many specimens studied, especially in *B. bufo*. Occasionally the morphologies of each species approach one another, and may even overlap, but it is still possible to determine each species using a combination of characters. Attempting to limit the morphological range for each species is difficult, but where there is uncertainty, other features which are described later may be used to reach a determination.

Viewed laterally, the tuber superior of *B. calamita* is usually almost straight-sided so that its apex is often pointed quite sharply, giving it a pyramidal appearance. Its sides are always smooth, concave or sometimes slightly convex, but never have lateral tubercles. The angle of these slopes is variable: generally less than 45^{o} in the modern specimens studied, but sometimes steeper. In specimens from Ightham (see Chapter 3.5 and Chapter 6.1), the tubers are very steep-sided, with sharp apices. Some specimens exhibit a subtle concavity in the slopes, with the narrow apex appearing more rounded as a result. Occasionally the posterior slope of the tuber is slightly less steeply angled than the anterior one and may even be slightly convex, giving the appearance that the apex is slightly anteriorly directed. In some fossil *B. calamita* (e.g. Figure 6.16f), there is a

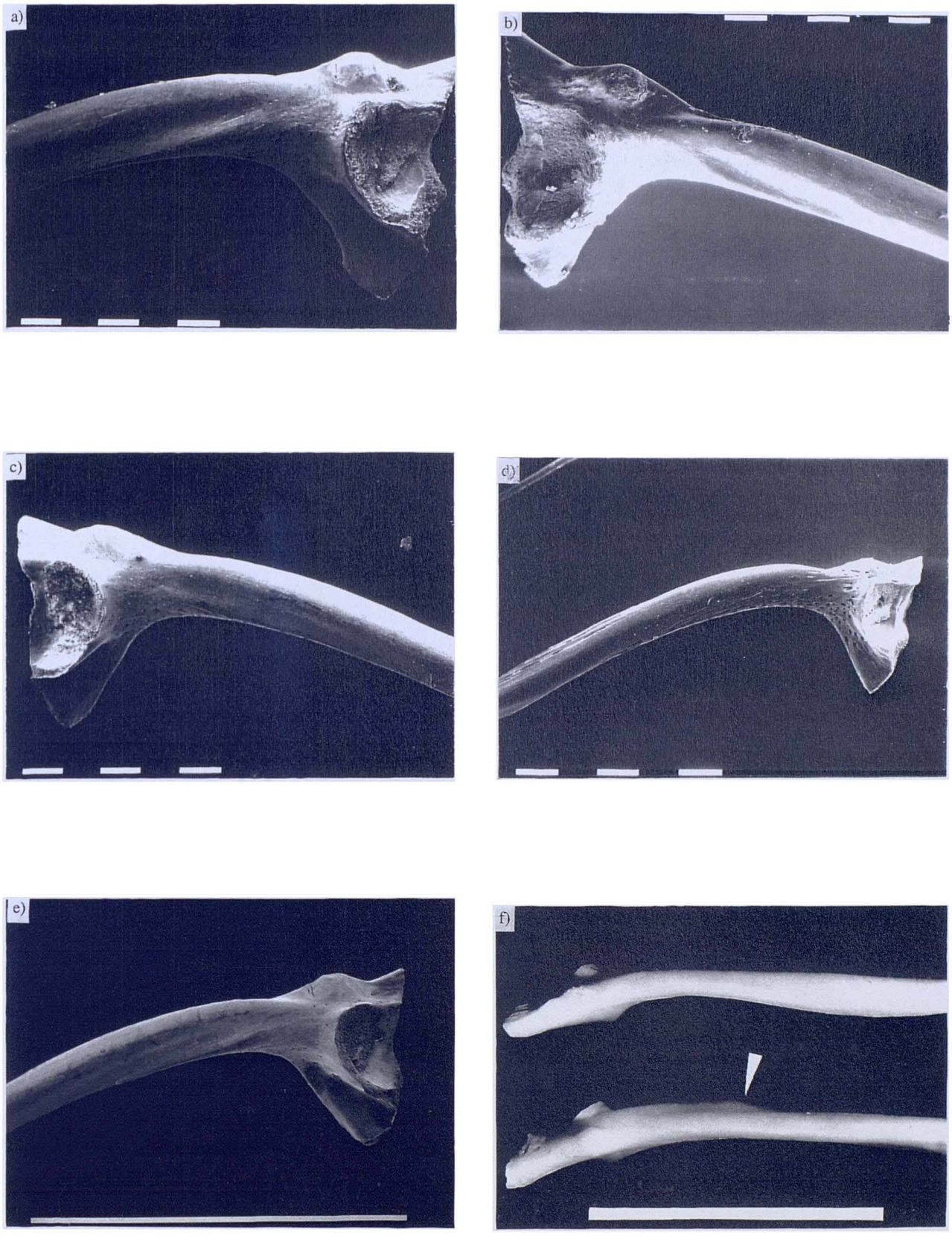


Figure 5.29: Lateral view (a-e) of: a) L. ilium of *B. bufo* (CGO 1/6); b) R. ilium of *B. bufo* (CGO 1/8); c) R. ilium of *B. bufo* (CGO 1/5); d) L. ilium of *B. bufo* (CGO 1/1, juvenile); e) L. ilium of *B. bufo* (CGO 1/???); f) dorsal view of left ilia of *B. bufo* (CGO 1/5) (top) and *B. calamita* (CGO 17/1) with ventrolateral crista arrowed.

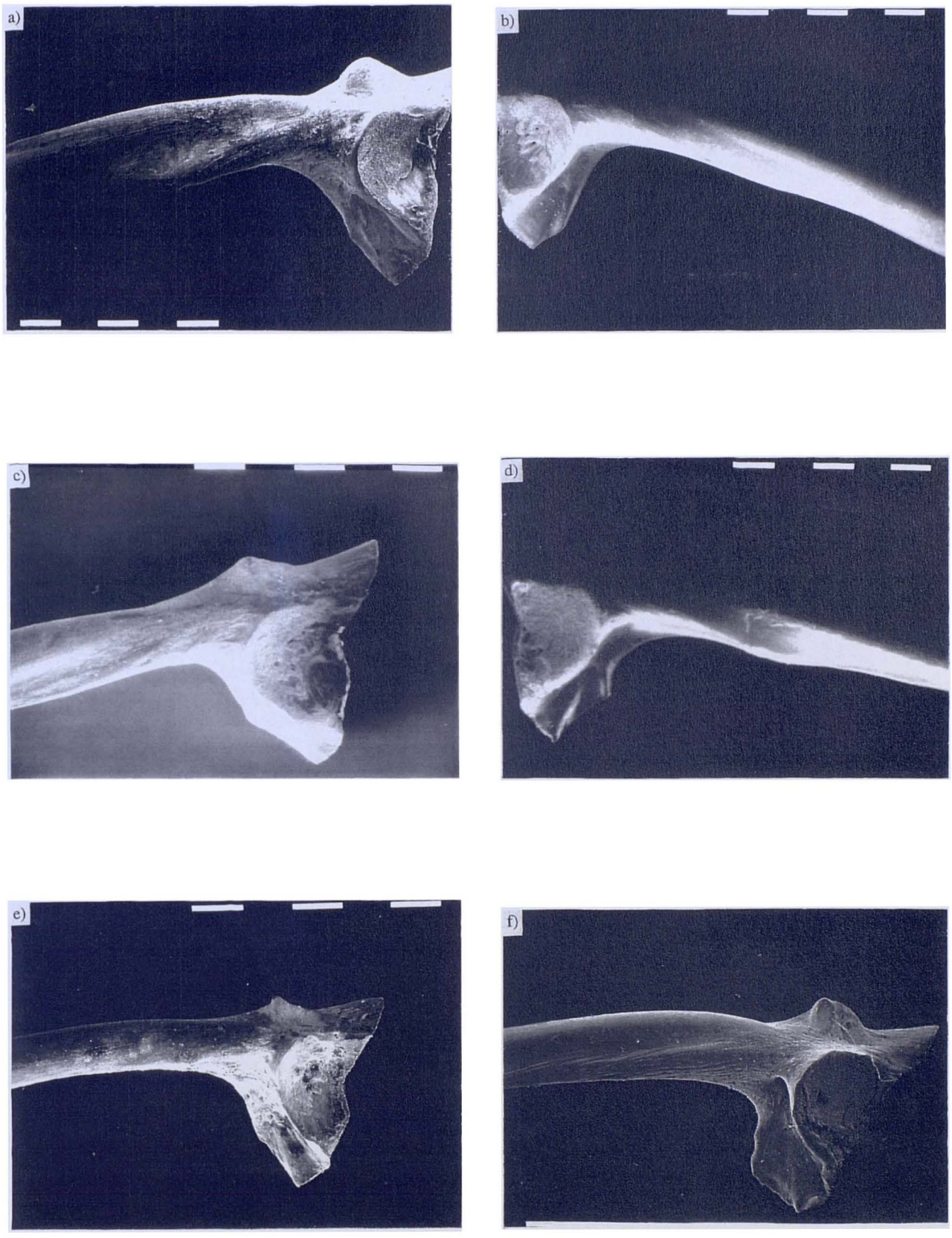


Figure 5.30. Lateral view of: a) L. ilium of *B. calamita* (CGO 17/1); b) R. ilium of *B. calamita* (CGO 17/7); c) L. ilium of *B. calamita* (CGO 17/7); d) R. ilium of *B. calamita* (CGO 17/2); e) L. ilium of *B. calamita* (CGO 17/9); f) L. ilium of *B. viridis* (CGO 29/1).

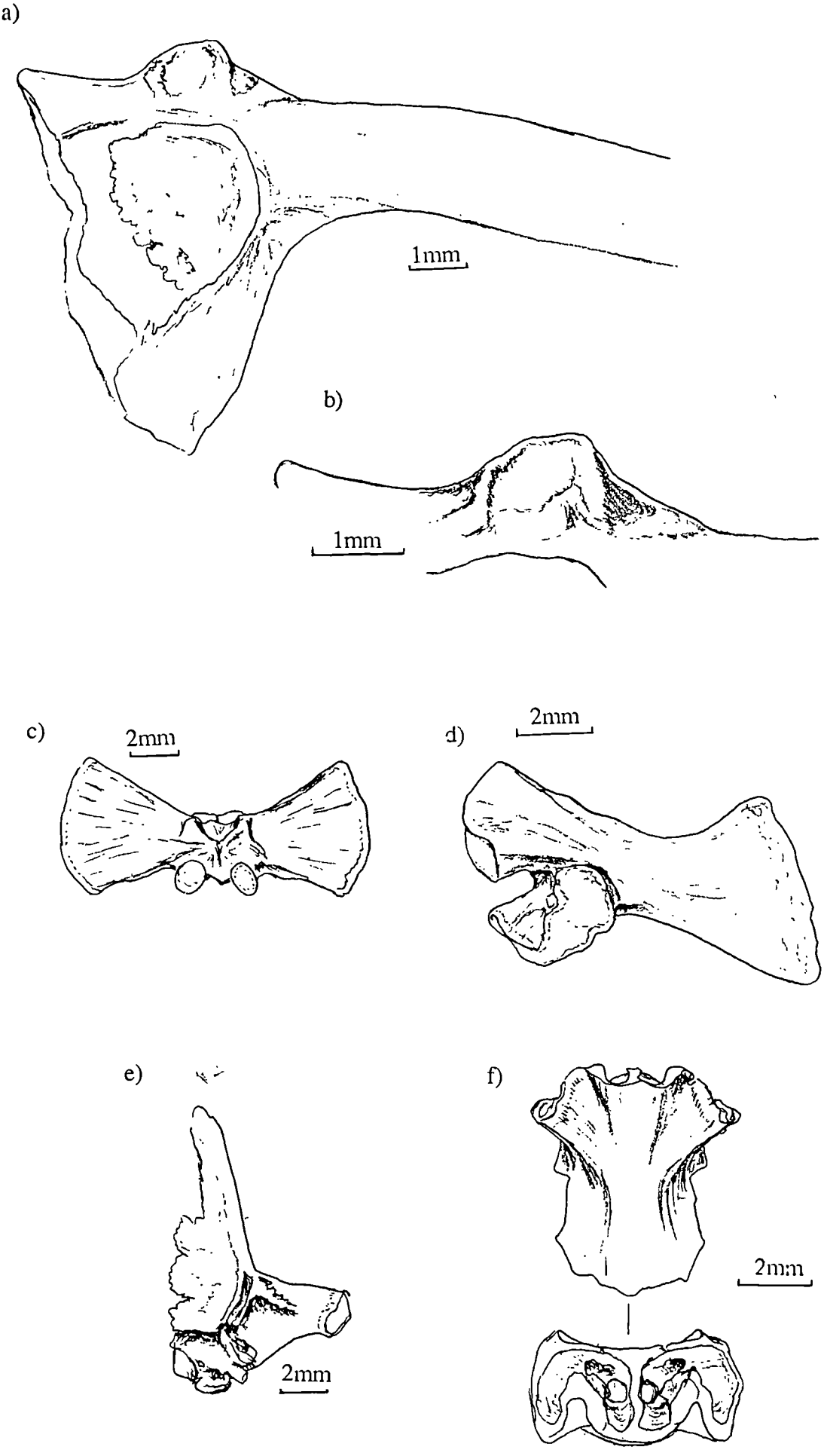


Figure 5.31: *B. calamita* (MNCN 15455, Spanish specimen): a) right ilium; b) detail of tuber superior; c) sacrum, dorsal view; d) left scapula, ventrolateral view; e) right frontoparietal/exoccipital/prootic, dorsal view; f) sphenethmoid, dorsal and anterior views.

Figure 5.32: Fossil left ilia of *B. viridis* from Late Pleistocene sediments of Ghar Dalam Cave, Malta (N R9555) (1mm scale).

fine ridge on the lateral side of the tuber, tapering dorsally to the apex. An additional pair of fine ridges may also radiate anterodorsally and posterodorsally on the lateral side of the tuber. From lateral view, the tuber in *B. calamita* tends to be more symmetrical than in *B. bufo*.

In *B. bufo*, the tuber is generally rounded and laterally bulbous. The apex is never as acute as in *B. calamita*, and is often shouldered. Most specimens studied have a somewhat rugose sub-rounded, or sub-cuboid tuber. The medial tuber face may be fairly smooth in *B. bufo*, but the lateral side is almost always protrusive, and often indented around its base. Its surface is generally indented with furrows, which accentuate the lateral protrusion. Using terminology of Chantell (1964), the broad base and shallower flanks of the tuber form the dorsal prominence, and the accentuated laterally protrusive (often sub-cuboid) bulb is the dorsal protuberance. Hodrová (1985) described the roughened tuber of *B. bufo* as being furnished with small tubercles.

Viewing the tuber from a dorsal or posterior aspect shows that in *B. calamita* the medial face tapers smoothly to the apex, whereas in *B. bufo* it is convex and roughened, with an uneven outline. Holman (1989b) noted an unusual form, in *B. bufo* from West Runton, where occasional specimens may exhibit a continuous, bladelike crest connecting a low pointed tuber to the pars ascendens and to the ala. Some Late Holocene specimens of *B. bufo* from Coveney (Lincolnshire) have tubers with a distinctively shouldered apex (see Chapter 6.4).

The tuber superior in *B. viridis* is prominent and normally divided into two or three coalescent peaks, with an overall more rounded apex than *B. calamita*. The sides are relatively straighter than *B. bufo*, and not laterally tumid. Viewed laterally, the tuber tends to lean anteriorly. Pleistocene specimens from Ghar Dalam Cave, Malta (Figure 5.32) exhibit a range of tuber forms, but all are distinct enough to separate them from the range of morphological variation seen so far in *Bufo*. The presence of a deep preacetabular fossa enables independent diagnosis in all cases.

Some specimens may have less distinctive features, and some overlap in superficial morphology may exist. However, observation of finer details can almost always provide a conclusive identification, using the tuber superior. One mature male *B. calamita* specimen (CGO 17/1) has a rounded tuber apex (Figure 5.30a), similar *B. bufo*, though its overall greater height and pyramidal form distinguishes it from *B. bufo*. In immature specimens of *B. calamita*, the tuber is relatively small, but more acute than in immature *B. bufo* where even juveniles have rounded tubers. In mature specimens, the ilium becomes more robust, involving thickening of the tuber, giving it a less sharply defined profile in some cases.

Ventrolateral crista

In all three species, the proximal half of the ala normally exhibits some flattening, produced in varying degrees into a ventrolateral ridge, with an oblique linear furrow above it. This crista was described by Sanchiz (1977) as the '*calamita* blade', but by Holman (1989b; 1992) as the '*calamita* ridge', and was considered diagnostic by both. From current observations, a strongly developed ridge with an associated furrow is often found in both modern and fossil *B. bufo*, and is

not peculiar to *B. calamita*. For this feature to be useful in diagnosis of *B. calamita* it must be strongly developed. In some cases, reliance on this as a diagnostic criterion (e.g. Holman and Stuart, 1991; Holman, 1992) is therefore unsafe. The feature is not well-developed in smaller specimens of *B. calamita*, and appears to become more prominent with ontogenetic maturity. In robust adult specimens, the ridge extends as a flange which breaks the ventrolateral profile of the ala, and is angled at its anterior end (e.g. Figure 5.30d). In such specimens, a well-developed ridge could be termed a blade (*sensu* Sanchiz, 1977). Separation from *B. bufo* would be possible, but as *B. viridis* can also exhibit a strong ridge along the ala, identification would require other features on the corpus to be intact, in order to separate *B. calamita* and *viridis* with certainty. When viewed dorsally, this protrusion is clearly visible, but the corresponding ridge of *B. bufo* is not (see Figure 5.29f). Not all *B. calamita* exhibit a prominent or angular blade, and *Bufo* specimens without a well-developed blade can not be diagnosed by this feature.

Pars descendens ilii

Holman (1992b) suggested that the pars descendens ilii is diagnostic, being more extensive in *B. calamita* than in *B. bufo*. Sanchiz (1977), on the other hand, stated that there are no significant differences between species in this part of the ilium. There is considerable variation in this region, causing significant overlap, but some useful diagnostic information can be drawn for use in conjunction with other features. The outline of the pars descendens in *B. calamita* is usually angled anteroventrally, forming an acute spina pelvis anterior (*sensu* Gaupp, 1896). In *B. bufo* it is usually more rounded, though there are exceptions (e.g. Figure 5.29a). In some specimens of *B. calamita*, the spina is connected to the base of the acetabulum by a radial ridge, with two adjacent depressions. This character is distinct in all of the larger specimens, but not in smaller ones, and apparently develops with ontogenetic maturity. The angle between the margo anterior of the pars descendens and the margo dorsalis of the pars ascendens approaches 90° in adult *B. calamita*, but is distinctly less in *B. bufo*. Even *B. bufo* ilia with an angular pars descendens have its margo anterior at an angle less than 90° with the pars ascendens.

B. viridis can exhibit considerable variation in this region, and may have a wide and angular pars descendens, with a prominent spina pelvis anterior (as in CGO 29/1; Figure 5.30f). Conversely, fossil specimens from Ghar Dalam Cave (Figure 5.32) have relatively narrow pars descendens without an acute spina pelvis anterior. As there is some inconsistency in this region, the character of the pars descendens should be considered in conjunction with other features.

Ala attachment

The ala appears to have a distinctive shape and angle of attachment to the corpus in *B. calamita*. In lateral view, its connection to the corpus is straighter, forming a very obtuse angle with the pars descendens (approaching 180°). This gives it a more continuous dorsal outline, on either side of the tuber, than in *B. bufo*. In *B. bufo*, the angle of connection is usually much less obtuse and the

dorsal curvature of the ala is greater. Böttcher (1994) noted the diagnostic value of measuring the height of the tuber, relative to a hypothetical line between the tip of the pars ascendens and the most dorsal margin of the ala. In *B. bufo* the tuber does not extend above the line, but does in *B. calamita* and *B. viridis*. Böhme (1977) noted that this angle of connection in *B. bufo* is acute, though less obtuse would probably be more appropriate. An ilium with parts of the ala or corpus missing, rests at a different angle to a complete specimen, and produces a parallax error when viewing features relative to each other from above. This should be considered during identification of incomplete specimens.

Vexillum

The vexillum is very rudimentary in *Bufo*, and not developed into a thin blade as in *Rana*. The dorsal surface of the ala in *B. bufo* has a low, medially-recurved vexillum. This overhangs the medial side of the ala, running for much of its length, but widest at mid-length. This is clearly visible in dorsal view, and is much less obvious in *B. calamita* (see Figure 5.29f), where the vexillum is somewhat flattened and normally only produced towards the anterior end of the ala. The relatively undeveloped vexillum in *B. calamita*, gives some specimens a slight angularity on the dorsal outline of the ala, in the mid-shaft region, compared with a smooth arch in *B. bufo*. In specimens with a strongly produced *calamita* blade, the ala thus appears widest mid-way along, and narrower proximally.

APPENDICULAR SKELETON

Humeri

The humerus in *Bufo* has generally similar proportions as in *Rana*. Though toads have much stockier hindlegs than frogs, their forelegs are very similar. The humerus is very similar when viewed from the front, but in posterior view, the articular facet appears much more medially displaced than in *Rana*. Thus the flat area behind the lateral crista (well-developed in males) is wide, and the area on the other (medial) side of the lateral facet is very narrow, corresponding to the nedial crista which is insignifiicant in *Bufo*. In *Rana*, the posterior side of thge humerus shows the articular facet to be more centrally placed, though still asymmetrical due to the lateral crista being wider than the medial one. From many fossil examples, it also appears that the condition of the lower articulation (ball joint) of the humerus is reliably diagnostic. In *Rana*, it remains well-preserved, but in *Bufo* it is usually worn, leaving perhaps half of the sphere intact. Thus, the worn appearance of the lower end of a humerus usually identifies it as *Bufo*. This apparent weakness in the cancellous bone of the humerus and radioulna (the elbow joint) seems to be a trait of *Bufo* only, as subfossil *Rana* humeri and radioulnae are more intact in this region.

Radioulnae

As for the humerus, the radioulna in *Bufo* is not very easily distinguished from *Rana*. The

olecranon area (posterior articulation with the humerus) is usually more truncated in *Bufo*, and the cross-section of the distal end may be useful. The following are some observations in *Bufo* radioulnae, but it is not certain that these are reliable diagnostic criteria. In *B. calamita*, the radioulna is more robust and thicker in section. Its dorsal outline is more sinuous and the distal articulations are much wider. In *B. bufo*, it is straighter is more symmetrical, along a linear axis. Also, the distal end (olecranon) is more bulbous in the latter, with a more rounded ventral outline. The foramen on the medial side is more deeply excavated in *B. bufo*, and the ventral outline of the olecranon is more angular in outline. A sectional view of the radius and ulna shows that in *B. bufo*, they are similar in size and relatively symmetrical about a medial axis. In *B. calamita*, the radius is disproportionately larger than the ulna and somewhat asymmetrical, in end view.

Femora

These are shorter and much more robust in *Bufo* than in other European anuran genera. The epiphyses are noticeably wider in *B. calamita*. They possess a strong ventromedial ridge which widens to a broad flattened area in the proximal part of the femur. In *B. calamita*, this area extends two-thirds of the way along the femur and its ventral edge is more irregular in outline. In *B. bufo*, the flattened area fades mid-way along the shaft. The ventral edge is most pronounced mid-way along its length in *B. calamita*, whereas in *B. bufo* it is strongest proximally and fades distally.

Tibiofibulae

The tibiofibula is generally more robust in *B. calamita*, and broader towards the epiphyses, but this is dependant on maturity and varies somewhat between specimens. Other independent characters are required, in conjunction with overall appearance, to use this element in specific identification. As is typical in the anurans, the tibiofibula consists of a shaft which bifurcates at both ends, forming paired tubes. The sub-rounded epiphyses vary in shape, but are fairly constant within species. At the proximal end, the tibial and fibial parts are similar in shape and size. In *B. bufo*, the tibial part is sub-trapezoid and the fibial part more ovoid than this. In *B. calamita*, both parts are ovoid in end view, and not parallel. The sectional view of the distal end is more uneven and potentially more characteristic. In *B. bufo* the larger tibial part is trapezoid in sectional outline, with a considerably smaller ovo-trapezoid fibial part. *B. calamita* has a less angular outline, with tibial and fibial parts being more similar in size. The diaphysis is often stronger in male specimens, having a sub-linear crista running its length. The cross-sectional shape of the diaphysis is flatter than in the frogs. A large foramen, the foramen nutritius (Ecker, 1889), passes obliquely through the middle section of the shaft. Its width is proportionally bigger in *B. calamita* than in *B. bufo*, perhaps relating to larger blood vessels and stronger leg musculature in the former. The foramen enters obliquely on its dorsal side (facing up in crouching position), nearer to the proximal end, and leaves the ventral side further along the shaft (towards the distal end). A groove is excavated adjacent to either end, this channel is noticeably deeper in *B. calamita*, continuing some way along

the diaphysis. From a lateral view, the diaphysis is seen to be swollen around this medial section, where the foramen nutritius passes through it. This swelling is generally more pronounced in *B. calamita*, as would be expected in order to maintain strength despite housing a wider foramen. Thus the thinnest parts of the tibiofibula, in lateral view, are between the middle of the diaphysis and the epiphyses.

Ippen and Heinrich (1977) detailed observations on pathological abnormalities in tibiofibulae and other appendicular elements for fossil *Bufo* and *Rana*. Conditions such as swollen shafts, due to healed breakages, appear to be relatively common in fossil anurans. During the current study, material from several sites has displayed pathological abnormalities, often consistent with recovery from what must have been severe injuries to every part of the body.

Metapodials and phalanges

The metacarpals and phalanges are essentially very similar in form, being tubular and flared at the ends. On comparison of individual corresponding elements between species of *Bufo*, *B. bufo* tends to have more slender bones than *B. calamita*. In most cases it is difficult to identify which particular element is being dealt with in fossil situations. Respective elements are relatively shorter and correspondingly more flared at their ends in *B. calamita*, but this varies depending on the digit. The conical distal phalanges are much shorter in *Bufo* than in *Rana*. They are wider at their proximal ends in *B. calamita*, with a stubbier appearance than *B. bufo*.

As in males of *Rana*, the second digit metacarpal in *Bufo* possesses nuptial tuberosities (cristata nuptia). However, in *Bufo*, the third digit metacarpal also has a linear crista along much of its middle portion. These ossifications develop on metacarpals of mature males, beneath the muscular nuptial pads of the opposable digits used during amplexus with females. Older, stronger males have correspondingly larger nodules on their metacarpals, as well as strongly crested humeri, scapulae and other elements. Second digit metacarpals of *Bufo* have only a fairly rounded cristata nuptia, as opposed to the elongate, gnarled ridge in *Rana*. In *B. calamita*, the metacarpal is cylindrical and very robust. It is constricted at its middle but is considerably widened at both ends. The distal end is somewhat bevelled and angled away from the linear axis of the bone. In *B. bufo*, the metacarpal is wider at its proximal end than its distal end, though overall it is more slender and more flattened than in *B. calamita*. The form of the crista itself is readily diagnostic of genus and possibly to species. In *Rana* the tuberosity is much more extensive and calloused, but in *Bufo* it forms a smaller nodular growth on the side of the diaphysis, which can be identifiable to species, especially in mature specimens. In *B. calamita*, the crista is an irregular nodule which extends as a sharp uneven ridge, towards both epiphyses, along the length of the metacarpal. Of the four male specimens examined, three exhibited a well-developed crista as described above, but these varied directly with size of the specimen (maturity). The fourth specimen (a 38mm sub-adult) lacked any form of crista. In *B. bufo*, the nodular part of the crista is similar to that of *B. calamita*, but the ridge is not as strongly-developed, tending to be less obvious or absent along the distal portion of

the metacarpal. Overall, the crista appears to be less well-developed in *B. bufo*, even in mature specimens. This might relate to muscular differences demanded by differences in lifestyle and locomotion, during the period of amplexus. Given that crista form and strength is dependant on maturity, specific determination should rely more on the shape of the metacarpal itself.

5.8 Hylidae

(*Hyla arborea, Hyla meridionalis*)

The literature dealing with the osteology of the European Hylidae is, like other anuran groups, of a fragmentary nature. Very little comparative study has been carried out, and relatively little fossil material has been described in Europe. Böhme (1977) studied only three individuals of *H. arborea*, illustrating several elements, but did not discuss specific diagnosis. Sanchiz and Mlynarski (1979) and Holman (1992b) briefly considered the separation of *H. arborea* and *meridionalis*. Boulenger's (1897-8) descriptions are also of some use. One comparative specimen (CGO 46/1) has been obtained. Several specimens of *H. arborea* (Ref. nos. MNCN 16213, 16216, 16218) and *H. meridionalis* (Ref. nos. MNCN 16226, 16227, 19636, 19637) were studied at the MNCN during December 1997.

CRANIAL BONES

Böhme (1977) illustrated the frontoparietal and sphenethmoid of *H. arborea* (see Figure 5.19i and 5.20h). These appear to be distinctive for the genus, but criteria for specific determination have not been isolated for these elements. Sanchiz and Mlynarski (1979) considered *H. arborea* and *meridionalis* to be very similar, and did not find diagnostic criteria for any cranial elements.

VERTEBRAE

The trunk vertebrae in *Hyla* are less robust than *Rana* and *Bufo*, with narrower transverse processes, laterally or slightly posteriorly directed (see Figure 5.33f). The vertebrae are relatively wider than in discoglossids, pelobatids and pelodytids, but have a roughly square shape. They have smaller, more gracile zygapophyses than in *Rana* or *Bufo*. The anterior neural arch is deeply excavated in a broad U-shape. The third vertebra has wide, distally flared transverse processes, with their flattened ends tilted obliquely, as in *Bufo*.

Sacrum

This has two posterior condyles, and moderately flared transverse processes (see Figue 5.33d). This gives the sacrum a superficially similar appearance to *B. bufo*, but the diapophyses are angled slightly posteriorly. Their anterior edges are thus laterally directed, forming an angle of 180º, and the posterior edges form a smaller angle than in *B. bufo*.

PECTORAL GIRDLE

Scapula

This element was figured by Hodrová (1981). It has its distal end noticeably wider than its proximal end. It is more gracile than any other genera described here, and its middle portion is narrowly constricted (see Figure 5.33e).

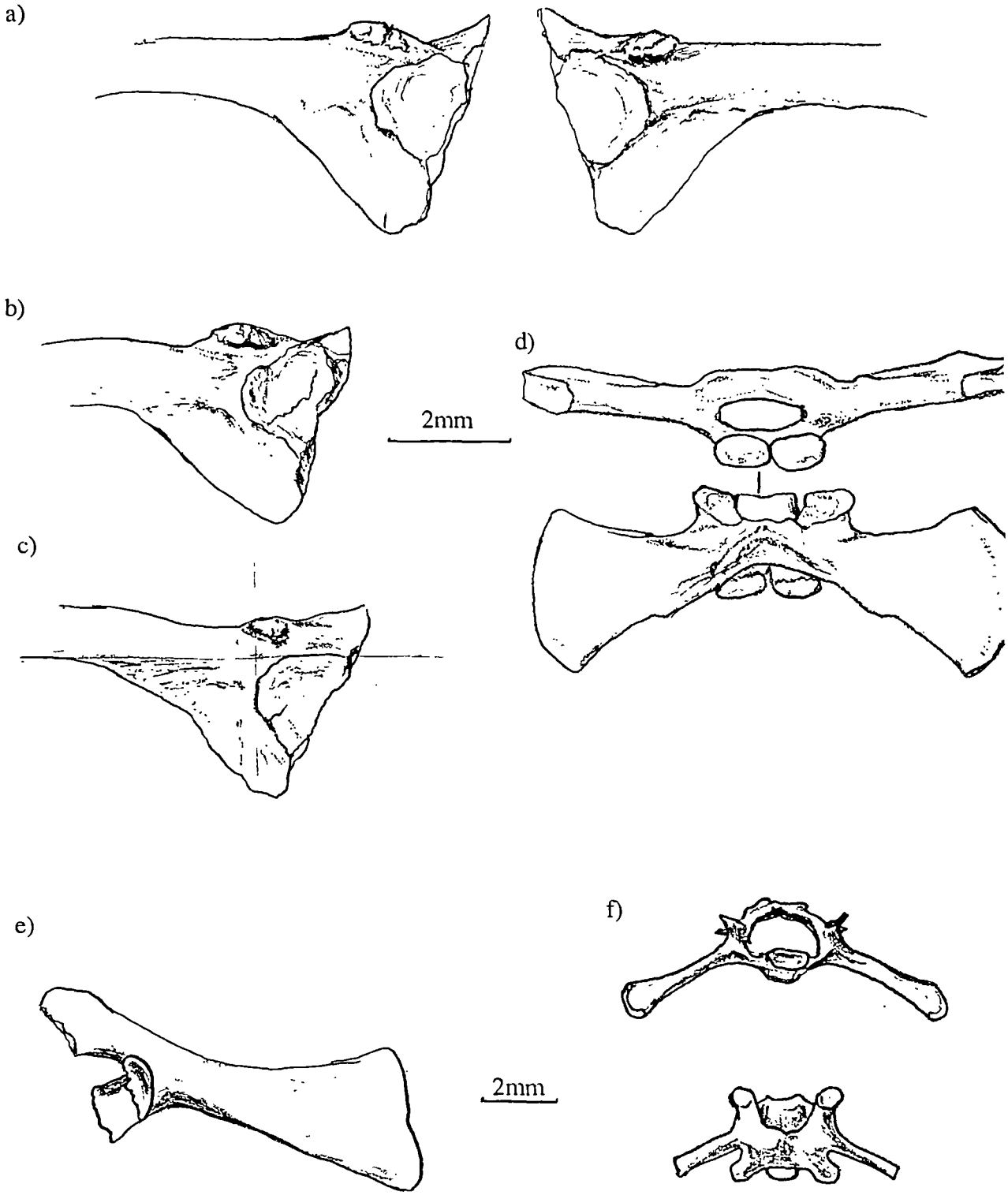


Figure 5.33: *H. arborea* (Spanish specimens): a) left and right ilia (MNCN 16216); b) left ilium (MNCN 16218); c left ilium (MNCN 16213); d) sacrum, dorsal and posterior views (MNCN 16216); e) left scapula, ventrolateral viev (MNCN 16216); f) third and ?eighth trunk vertebrae (MNCN 16216).

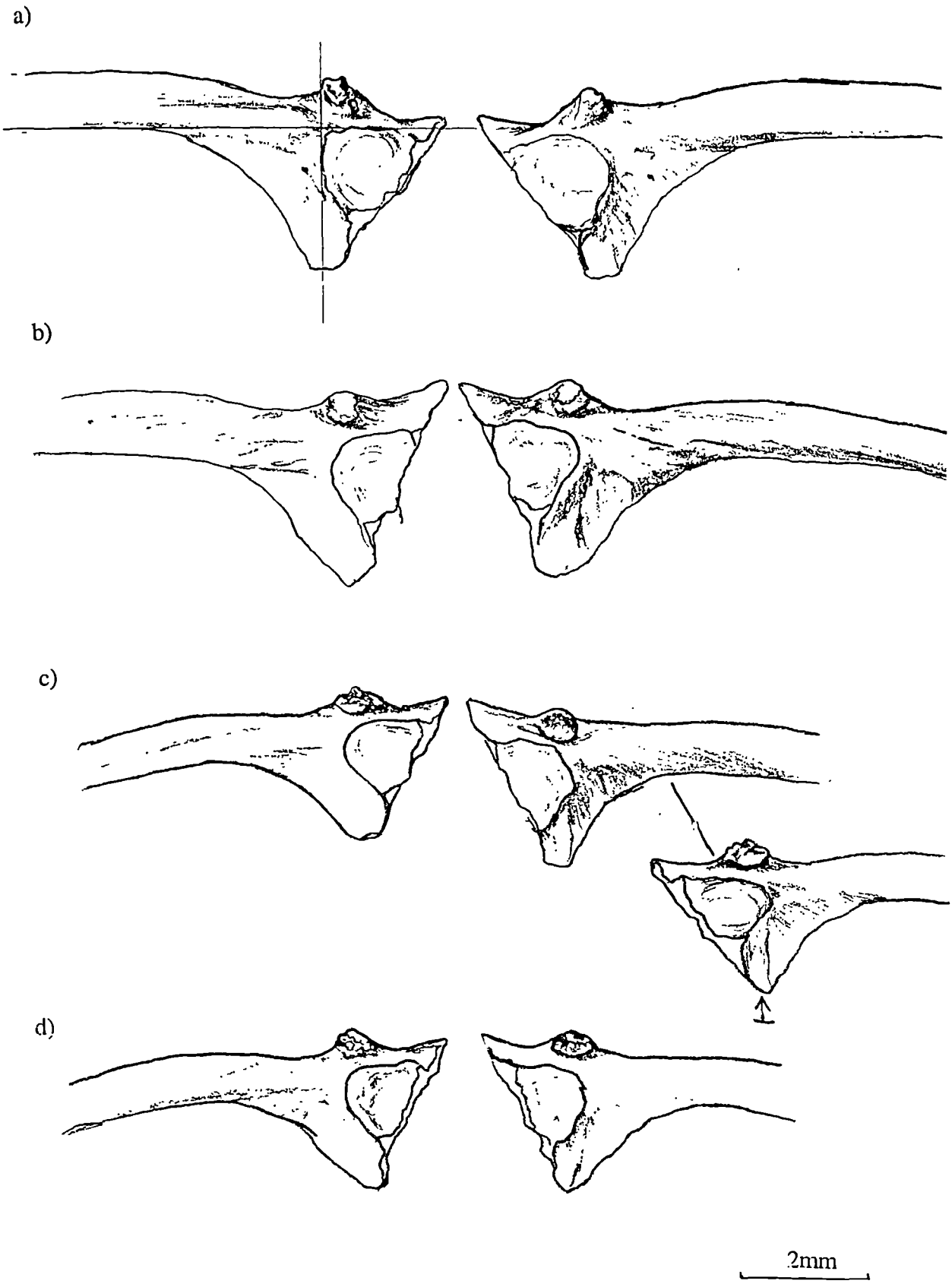


Figure 5.34: Left and right ilia of *H. meridionalis* (Spanish specimens): a) MNCN 16227; b) MNCN 16226; c) MNCN 19637; d) MNCN 19636. (2mm scale)

PELVIC GIRDLE

Ilium

The morphology of the ilium has been discussed by several authors. Sanchiz and Mlynarski (1979) found *Hyla* ilia to be highly characteristic in several characteristics. There is most noticeably a thin lamina connecting the pars descendens to the proximal portion of the ala. This was referred to as the ager limitans anterior by Böhme (1977), using terminology of Vergnaud-Grazzini (1966). Sanchiz and Mlynarski (1979) viewed this region as an extension of the pars descendens ilii. It is clearly a distinctive feature, making the ilia of *Hyla* easily recogniseable.

Hyla ilia have a pronounced tuber superior, though its form is evidently very variable (Sanchiz and Mlynarski, 1979; Holman, 1992b). Sanchiz and Mlynarski (1979) studied twelve individuals of each species, but were unable to find any diagnostic criteria for separation. Hodrová (1981) identified Pleistocene fossil *Hyla* ilia, with a range of variation in the tuber superior, from low and smooth to a very high ossicle with minute tubercles, but did not attempt specific determination. Holman (1992b), on the other hand, studied a total of fourteen *H. arborea* and *meridionalis* skeletons, and was able to differentiate between the ilia of both species. He used terminology from Chantell (1964) to characterise the form of the tuber for both species. In *H. arborea*, he described a low dorsal prominence with a superimposed dorsal protuberance (collectively equivalent to tuber superior). In *H. meridionalis*, the protuberance was found to extend laterally from the tuber in a distinctive way.

The single specimen of *H. arborea* obtained has very laterally directed tuber superiors, with roughened apices, and 'furnished with small tubercles' as described by Hodrová (1981). The ventral edge of the apex protrudes more than the dorsal edge. The MNCN specimens support these observations. The tuber is overall more elongate and less protrusive in *H. arborea* than in *H. meridionalis* where it is more compact. In *H. meridionalis*, the tuber is also more dorsolaterally produced, and has a rougher, more tuberculous apex. B. Sanchiz has recently studied thirty specimens of each species, and reached the same conclusions: that the tuber is lower and more elongate in *H. arborea*, short and more protrusive in *H. meridionalis* (Sanchiz, pers. comm., 1997). Holman (1992b) identified a fossil ilium from Itteringham (see Chapter 3.3) as belonging to *H. meridionalis*. Due to the difficulties of identifying *Hyla* ilia, this material was re-examined in October 1997 and Holman's identification is tentatively supported.

APPENDICULAR SKELETON

Humeri

Holman *et al* (1990) suggested that the humeri of *Hyla* could be identified by their straight, narrow shaft and small rounded distal condyle (see Figure 3.6c).

5.9 Ranidae

(Rana temporaria, Rana arvalis, Rana dalmatina, Rana ridibunda, Rana lessonae, Rana esculenta)

Without doubt, the anurans have received more attention in the literature than the other amphibian and reptile groups. The two volumes of Boulenger's 'Tailless Batrachians of Europe' (1897-8) examined in turn twenty three species of frogs and toads (anurans) with descriptions and figures of their skeletons. This included *Rana*, but some taxonomic changes have occurred since its publication. Ecker (1889) examined the osteology of *R. esculenta* in detail and other workers have detailed certain aspects of skeletal form in anurans (e.g. Parker, 1871; Gaupp, 1894).

Very little literature has dealt with the osteology of individual species on a comparative basis. Böhme (1977) summed up the history of such work and highlighted the problems of uncertainty over identification, particularly of the green frogs. This was reiterated by Böhme and Günther (1979) who found that diagnosis using the ilium was not conclusive, but that frontoparietals were diagnostic. The nature of most fossil material, which generally consists of isolated bones that are often broken and eroded, can make identification very difficult. Owen (1990) and Strenski (1995) carried out MSc studies on *Rana* remains from some of the Creswell Caves (Derbyshire) and the Kitley Caves (Devon), repectively, but neither was very conclusive in their determinations.

Böhme (1977) has produced the most useful osteological comparison of the European Ranidae, with well-drawn figures of several skeletal elements. He made a detailed comparative ostelogical study (in some cases based on more than twenty skeletons of each species), and attempted a descriptive key for the diagnosis of the European anurans. Unfortunately, the key is poor, and as his descriptions are short and often ambiguous. Thus they are of very little diagnostic value.

Böhme (1977) considered only the frontoparietals and ilia to be diagnostic elements. It is not clear whether he took into account the entire skeleton in his study (this would undoubtedly have been a major task), but he stated clearly that he was unable to identify the green frogs on the basis of the ilia (Böhme, 1977). This must be borne in mind when using the drawings provided in that paper, especially as they were re-drawn by an artist from Böhme's original drawings. Holman in many of his publications seems to have relied heavily on these drawings, and does not appear to have undertaken his own osteological studies with comparative material. The current author concludes that visual comparison with reference specimens is essential in order to reach an unbiased diagnosis of fossil *Rana* material. B. Sanchiz is currently preparing an osteological identification key for the European Anura, with detailed drawings and biometric measurements (Sanchiz, pers. comm., 1997).

Twenty specimens each of *R. ridibunda* and *R. esculenta*, three *R. lessonae*, four *R. arvalis* and twelve *R. temporaria* have been examined in the current study. English Nature provided green frog specimens and C. Snell provided *R. arvalis*. No specimens of *R. dalmatina* have been obtained, though one disarticulated skeleton was studied during a visit to the PAS. Not all skeletal

elements have been considered and some have been considered in more detail than others, according to observed occurrences in the fossil record. Comparison with *Bufo* forms the basis of much of the description. For reliably diagnostic elements, separation to species is described where possible. Osteological terminology follows that of Vergnaud-Grazzini (1970) and Böhme (1977) in most respects, but with modifications from Sanchiz and Mlynarski (1979).

CRANIAL BONES

As six species of *Rana* are being considered, many cranial elements do not possess enough character to be diagnostic.

Exoccipitals

These paired bones form the back of the cranium, and the occipital condyle surrounding the foramen magnum. Although Trueb (1973) suggested that the otoccipital (i.e. exoccipital and prootic) is indistinguishably fused in recent anurans, this is not the case in many European species. In *R. temporaria*, more than other European species of *Rana*, the exoccipitals are sometimes fused firmly to the prootics or even other bones, but not normally in the other species. This may be an aid to identification if these bones are found as fossils in such a way.

The internal fenestrae within the framework of the exoccipital are very variable in shape, size and number (normally two but sometimes coalescing into one) and it is unlikely that diagnostic information can be drawn from these. When viewed posteriorly, the width of the exoccipital is seen to be closely related to ontogenetic position. The width of a frog skull obviously becomes greater in relation to its height with age. In the *R. arvalis* specimens seen, the exoccipital may be more rectangular in posterior profile than *R. temporaria*. However, the range of *R. temporaria* specimens seen has shown that this is a very variable species and reliable separation has not been achieved for this element.

Squamosals

The squamosal in *Rana* has a T-shaped form, with the horizontal part directed axially. The anterior arm connects with ligaments, and the posterior one to the prootic. The vertical arm is directed posteroventrally, and connects with the quadratojugal. Ecker (1889) noted that the anterior arm is shorter in *R. temporaria* than in *R. esculenta*, and referred to it as the processus zygomaticus. In the specimens studied here, the anterior arm is longer in *R. ridibunda* and *R. esculenta* than in *R. temporaria* and *R. dalmatina*, and more pointed. The limited *R. lessonae* available do not have significantly longer anterior arms than the brown frogs.

There is noticeable intraspecific variation in this bone, with considerable differences in shape and proportion, though some features seem to be constant. There is a dorsal ridge running from the anterior process to the posterior one. In the brown frogs, this ridge is situated dorsally and is not as sharp, becoming weaker towards the posterior process tip. In green frogs, the ridge is more

dorsolaterally placed, sharper and more extensive. The vertical arm is narrower in green frogs, with a stronger medial ridge running its length. The ventral end of the upright arm is variable in shape, but there seems to be some useful consistency. In the green frogs, it is more angular than in brown frogs, and often has three clear corners. This gives it a trowel-shaped appearance. In the brown frogs, the lower end is more spatulate, with a rounded tip, and no sharp corners. Further specific diagnosis would require a larger collection of reference specimens, but it appears that the descending arm of the squamosal is narrower towards its base in *R. lessonae* than in the other green frogs.

Angulosplenials

The coronoid process is generally stronger and more shouldered than in *Bufo* which has a smoothly rounded outline. The coronoid process is more robust at its anterior side, and thins into a blade towards its posterior margin. Thus, in some cases where resorption must have taken place, this gives a fin-like appearance to the process. The lateral sulcus (for receiving the Mentomeckelian cartilege) is shallower in *Rana* than in *Bufo*. Its dorsal margin continues as a well-defined ridge to beyond the coronoid process, whereas it terminates at the coronoid process in *Bufo*. Towards its posterior end, the ventral edge of the angulosplenial expands laterally as a horizontal flange. In *Rana,* this only occurs posterior to the coronoid process, in *Bufo* a wide horizontal flange extends beneath the coronoid process to join the lateral sulcus.

Dentaries

These have a wide rounded medial end. The dorsal surface is deeply concave and the middle section is much more constricted than in *Bufo*. The lateral end is somewhat flattened and flared, with the Mentomeckelian cartilege correspondingly wide and tapering to a fine point. The medial tip of the dentary widens more abruptly and is cup-shaped in the green frogs.

Frontoparietals

These elements are quite distinct between species, and as shown by Böhme (1977) and Böhme and Günther (1979), are reliably constant within species. The frontoparietals of *Rana* are easily distinguished from *Bufo*, in that the latter always have a deep groove separating the pars parietalis from the area which connects with the prootic and exoccipital. The bone is generally elongate and tapers anteriorly. Specific determination is possible using the frontoparietals (Böhme, 1977; Hodrová, 1981). Those of the green frogs are narrower and more elongate in the pars frontalis. The illustrations in Figure 5.19 give an indication of the characteristic shapes. Böhme and Günther (1979) studied green frog frontoparietals in detail, and found them to be a reliable element for specific identification (more so than ilia). The thickness of the bone (seen in cross-section) was much greater for *R. ridibunda* than for *R. lessonae,* in which the bone is thin and relatively fragile. *R. esculenta* was intermediate between these two forms.

Parasphenoid

This cruciform bone forms the floor to the cranium, but is thin and easily broken. It is relatively featureless and its shape is not very useful for diagnosis. In *Rana*, it is more slender, with longer anterior and transverse lobes than in *Bufo*, but as this element rarely survives intact as a fossil, this character is not often of use. Within *Rana*, the green frogs tend to have a much longer, and relatively narrower, anterior lobe. This is of a similar width to the transverse lobes, whereas in brown frogs, the anterior lobe is wider. The short posterior lobe is wide, but truncated abruptly in green frogs, but angled to a point in the brown frogs. Further diagnostic information might be achieved by detailed study of the surface relief of this element.

Pterygoids

No firm diagnostic criteria have been found for this element. It is often found incomplete as a fossil and is of little value here.

Maxillae

Together with the premaxillae, these form the upper jaws. They bear teeth in *Rana*, which easily separates them from the toothless *Bufo*. They are not diagnostic of species, however, and are generally preserved in fragmentary condition.

Premaxillae

Again, these bear teeth in *Rana* (unlike *Bufo*), but distinction beyond this has not been possible. Specimens of *R. ridibunda* have up to twelve teeth on each premaxilla, and up to eight in *R. esculenta*. This may be a direct function of age and size, as additional teeth appear to be added between existing ones. Further work would be required to assess whether this character is of any use in diagnosis.

Hyoidal cornua

The cornua of the hyoid are fairly fragile bones, and are more slender and less robust than in *Bufo*. In green frogs, the posterior ends of the cornua are more widely flared than in brown frogs.

VERTEBRAE

As with almost all anurans, there are nine vertebrae: an atlas, seven trunk vertebrae and a sacrum. The urostyle is a coccygeal extension which is here classed as part of the vertebral column. Vertebrae appear to be the elements most affected by pathogenic and congenital deformity. It has been noted on several occasions (e.g. Böhme, 1982; Bourne, 1884) that asymmetry, fusion and malformation of vertebrae are fairly commonplace in *Rana*. Fusion most commonly takes place between the eighth trunk vertebra and sacrum. Older individuals often show signs of tubercular growth on transverse processes. This has been seen in both sexes of *R. temporaria*.

Atlas

The dorsal surface may exhibit a neural spine and posterior neural arch with the same characters described for trunk vertebrae below. However, it is sometimes incompletely ossified here, so that a wide canal or even a fissure runs along it axially. The condylar facets are typically widely flared in *Rana* and more ovate, rather than subrectangular as in *Bufo*. They are also more concave and tilted upwards in *Rana*.

Trunk vertebrae

Trunk vertebrae are quite variable in proportions, particularly in the size of their transverse processes. In *Rana*, the transverse processes are robust and directed anteriorly in the second vertebra (first trunk or axis vertebra). They are much wider in the third vertebra, directed transversely but downwards, and are flared at their ends with an additional spine on the posterior edge. The fourth vertebra has has robust posteriorly directed processes. The fifth to eighth vertebrae have smaller, thinner processes, all tilted upwards. The fifth and sixth have their processes directed posteriorly, the seventh and eighth more or less transversely. The centrum of amphibian vertebrae holds information considered very important to systematics and phylogeny. Depending on the concavity or convexity of the vertebral ends, vertebrae are known as procoelous (concave anterior end), opisthocoelous (both ends convex) or amphicoelous (both ends concave). In *Rana*, the first seven vertebrae are procoelous, the eighth (last trunk) vertebra is amphicoelous and the sacrum is opisthocoelous.

Morphology seems consistent in some ways within species, but *R. temporaria* is highly variable and isolation of diagnostic criteria is not simple. *R. temporaria* trunk vertebrae have a low, sometimes thick, rounded neural spine. In some cases it may be reduced or indistinct. The dorsal surface is always convex, and may be bulbous in the dorsolateral regions. This can separate it from *Bufo*, which has a sharp and well-developed neural spine, and tends to have flat or concave areas in the anterolateral parts of the dorsal surface. *Rana* vertebrae also possess a transverse ridge across the dorsal surface. This may be low and rounded, or fairly sharp, tending to be lean posteriorly, with its posterior flank excavated on either side above the posterior neural arch. This may give it a shallow anterior slope, and a steep, concave posterior side. In the green frogs, the neural spine tends to be better defined, more posteriorly directed and raised into a crest, often extending over the posterior edge of the neural arch. The third and fourth vertebrae of all species have their neural spines tapered into a posteriorly directed tubular crest. This is least distinct in *R. temporaria*. In the green frogs, the crest is far more produced and its tip reaches well beyond the posterior margin of the neural arch, especially in the third vertebra.

The anterior margin of the neural arch is sharply indented in a V-shape in the green frogs, but has only a slight concavity in *R. temporaria* and *R. arvalis*. The neural arch itself has a variable shape, and may be rounded or vaulted, but this does not appear to be reliably constant within species. Immature animals have much more slightly built vertebrae, with a very short centrum

length, a very large neural canal, and thin neural walls. These become more robust with maturity, and the relative size of the neural canal decreases. Immature *Rana* still possess the neural spine characteristics of adults of the species. For example, young green frogs have a very small neural spine, but it is well defined and posteriorly directed.

The third vertebra (second trunk vertebra) has particularly wide transverse processes, which are flared towards the ends and usually have an extra spine produced on their posterior edge (see Figure 5.35). In *R. arvalis*, the neural spine of the third vertebra can be strongly developed into a posteriorly directed tubular crest. This character, together with the strong transverse processes, can be indistinguishable from *R. ridibunda* and *esculenta.*

Its transverse processes are much shorter and thinner than the equivalents in the *R. ridibunda* and *esculenta* specimens seen. This is easily observable, as the vertebra lies flat on the base of its centrum, whereas in both *R. ridibunda* and *esculenta*, only the posterior end of the centrum will rest on a flat surface.This is due to the downwardly directed transverse processes extending below the level of the centrum in these species. The transverse processes in *R. ridibunda* and *esculenta* are longer and more curved downwards and backwards.

Sacrum

The sacrum has a pair of robust, tubular transverse processes, which are directed posterolaterally and somewhat tilted upwards (see Figure 5.36). These articulate with the anterior tips of the ilial alae. There is a low neural spine, but it is mostly absorbed within the sinuous transverse ridge. The ridge is well defined in all species, and tends to have an acute crest which is angled anteriorly.

Urostyle

The urostyle of *Rana* is not dissimilar to that of *Bufo*. It has a high and continuous dorsal ridge (crista dorsalis), flanked by sloping laminae which enclose the vertebral canal. The anterior tip of the dorsal ridge leans forward in *Rana*, overhanging the opening of the vertebral canal. In *Bufo*, the ridge tip tends to lean backwards. On each lateral flank, close to their anterior (and highest) end, one or two apertures open into small coccygeal canals. These enter obliquely into the anterior part of the vertebral canal, but their shape and size is variable. According to Ecker (1889) they are generally larger in *R. esculenta* than in *R. temporaria*. Their position and size may offer some diagnostic information, but not without use of additional features.

PECTORAL GIRDLE

Scapulae

These are often well preserved as subfossils, and in *Rana* have a distinctive dorsomedial ridge, produced very strongly along much of its length. The outline of the scapula is trapezoid, and constricted at its middle, so that the margo anterior and margo posterior are concave. In the green frogs, the ends are more flared, with the middle being relatively narrower than in the brown frogs.

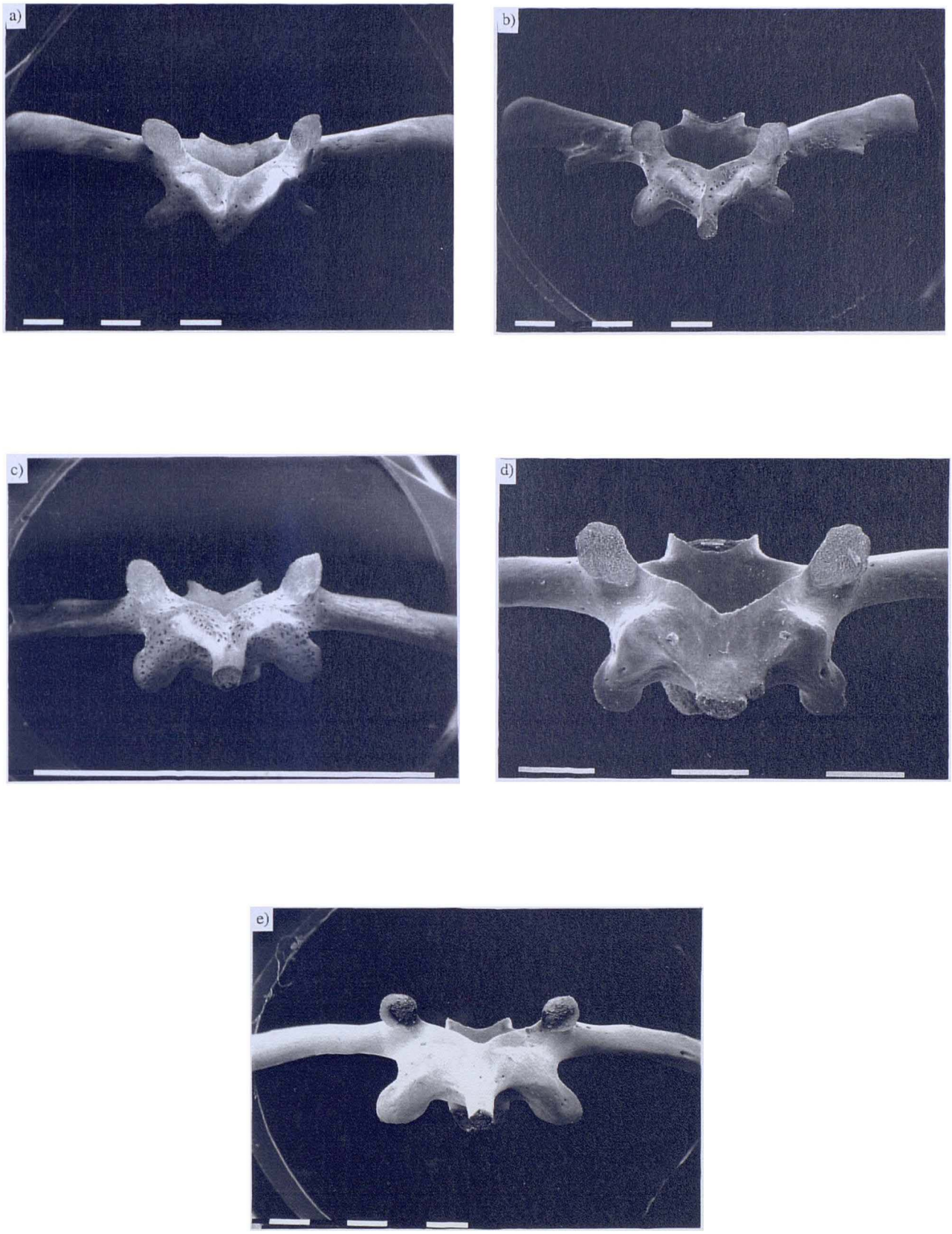


Figure 5.35 Third trunk vertebra (dorsal view) of: a) *R. temporaria* (CGO 2/21); b) *R. arvalis* (C. Snell coll., 60mm); c) *R. ridibunda* (CGO 42/1); d) *R. lessonae* (J. Buckley coll.); e) *R. esculenta* (CGO 44/4).

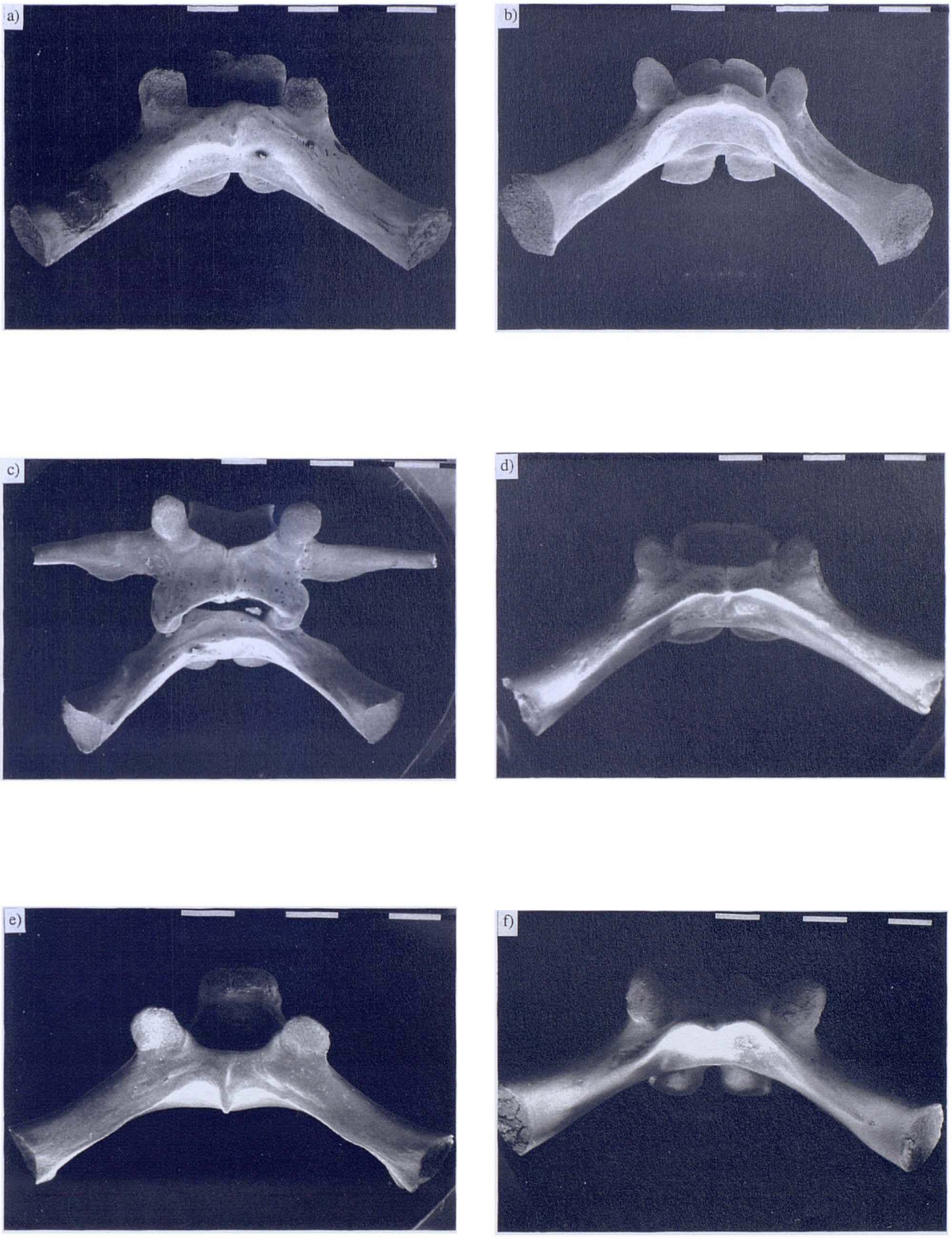


Figure 5.36:Sacrum (dorsal view) of: a) *R. temporaria* (CGO 2/21); b) *R. temporaria* (CGO 2/23); c) *R. arvalis* (sacrum fused to eighth vertebra, C. Snell coll., 60mm); d) *R. ridibunda* (CGO 42/1); e) *R. lessonae* (J. Buckley coll.); f) *R. esculenta* (CGO 44/4).

This seems to conflict with the observations of Hodrová (1981) who noted that *R. lessonae* and *esculenta* have a less concave margo anterior. The brown frog scapula is more elongate, with its ends narrower and more oblique. The distal articulation with the suprascapula is straight or convex in brown frogs, but noticeably concave in green frogs. In posterior view, the scapula is more strongly curved in brown frogs, with a much better-developed dorsomedial ridge, particularly in *R. temporaria*. The shapes and configuration of the proximal articular surfaces may be useful in diagnosis but this would require more detailed analysis and is likely to exhibit some intraspecific variation. Within the brown frog group, *R. arvalis* has a more slender scapula than *R. temporaria*, particularly in its middle portion, giving it a more gracile form. *R. temporaria* has an overall thicker and more robust scapula than the other species. Hodrová (1981) also noted that *R. arvalis* has a distinctive pars acromialis, but this has not been observed conclusively.

Sternum

The sternum is a thin, flat plate, positioned anterior to the symphysis between the coracoids. Its shape is subrectangular, with concave left and right sides. In the green frogs, the sides are much less concave, and may have an almost perfectly rectangular shape. This is due to the presence of thin, sharp laminae filling the concavities on both the left and right sides. In the brown frogs, the sides are more concave, and the ends noticeably flared, giving the centre of the sternum a more constricted appearance.

Omosternum

This element is shown in Figure 5.37. This is noticeably more robust in males, which corresponds with an overall stronger pectoral girdle than in females. It has a medial ridge, running along its ventral surface, and its proximal end is flared. In males the proximal end is thickened and the ventral ridge is stronger, giving the bone a triangular cross-section in brown frogs. In the green frogs, the proximal part is more flattened, especially in *R. ridibunda*. In *R. lessonae*, this end is not as wide as in *R. ridibunda* and *R. esculenta*. As would be expected, the character differences between the three species are probably gradational. As the omosternum of *R. lessonae* is narrower than the other green frog species, not as vertically thickened and has a narrower ventral crista than in the brown frogs, the isolation of *R. lessonae* should be possible.

In brown frogs, the ventral ridge extends to the proximal tip of the omosternum, where the bone is thicker and more triangular in cross-section than the green frogs. Here the ridge may bifurcate, exposing cancellous bone. The posterior edge is generally squarer and more shouldered in the brown frogs, whereas the tendency in the green frogs is for an arcuate posterior edge. In females, the bone is flatter and the features weaker, but diagnosis to green or brown frog group might still be possible.

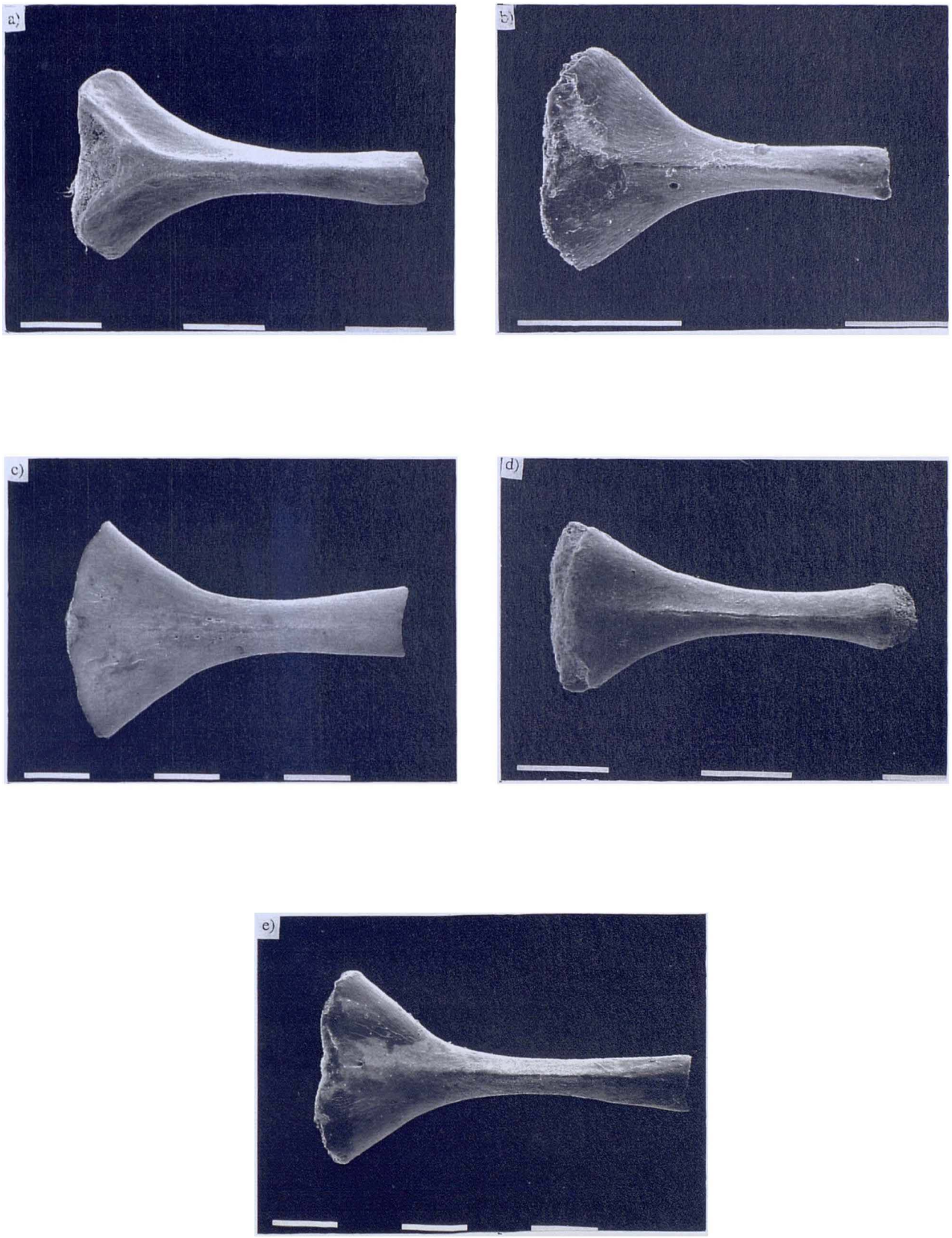


Figure 5.37 Omosternum (ventral view) of: a) *R. temporaria* (CGO 2/2); b) *R.arvalis* (C. Snell coll., 42mm); c) *R. ridibunda* (CGO 42/18); d) *R. lessonae* (J. Buckley coll.); e) *R. esculenta* (CGO 44/2).

PELVIC GIRDLE

Ischium

Though this bone ossifies well, and is often preserved subfossil, its form is not distinctive between species. Its overall shape is semicircular, extending ventrally well below the acetabular margin. There are probably subtle differences which would isolate *Rana* from *Bufo*, but useful diagnostic features have not been found.

Ilium

The ilium has been the most used element in the diagnosis of fossil *Rana*. However, as the taxonomic status of species within the genus is uncertain (Sanchiz and Mlynarski, 1979), isolating true diagnostic characters from ilia is not simple. *Rana* ilia have a distinctive tuber superior which rises anterodorsally from the anterodorsal part of the corpus. It is connected to the ala, in varying degrees between species, by a blade-like vexillum. Vergnaud-Grazzini (1970) used the form of the tuber superior and vexillum to separate *R. temporaria*, *R. latastei* and *R. esculenta*, but at that time, the status of the three green frog species was not understood. Böhme (1977) attempted a brief descriptive key for the identification of *Rana* ilia, but this is too simplistic, judging by the material seen so far. Several features noted by Böhme are very useful in separating at least some of the species, but difficulties arise due to the large degree of morphological variation found particularly in *R. temporaria, R. ridibunda* and *R. esculenta.* Böhme (1977) studied at least twenty specimens of each green frog species, and yet concluded that they could not be separated using the ilium. Böhme and Günther (1979) carried out a more extensive study on modern and sub-fossil material, using biometric methods, which permitted some specific diagnosis. The range of variation found within them is likely to be gradational, due to their shared genetic character. Some morphological traits are distinctive in the parent species, but these appear to be blurred in the different forms of *R. esculenta*, which can not as yet be identified from living animals without genetic testing.

See Figures 5.38-5.47 for comparison of the useful diagnostic features.

The brown frogs can be fairly easily separated from the green frogs using the thickness and shape of the junctura ilioischiadica (Figure 5.47). Böhme (1977) noted this, and suggested the use of a relative corpus thickness ratio. From the current studies, it appears that both *R. temporaria* and *R. arvalis* can be separated from the green frogs. The junctura in green frogs tends to be thicker, with a more stunted pars descendens and higher acetabular sides, particularly the ventral side. The brown frogs are characterised by a more slender junctura outline, and lower acetabular sides. Measurement of the ratio between the acetabular diameter (d), and the corpus thickness at the centre of the acetabulum (t), confirms this. The d/t ratio in the green frogs studied ranged from 2.12 to 2.88, and from 2.75 to 4.00 in the brown frogs. Only one specimen was responsible for the overlap. The mean d/t ratios for each group show clear groupings, and represent characteristic corpus thicknesses. In all green frog ilia seen, the junctura is thicker, and the ventral wall of the acetabulum is raised higher than the dorsal wall, thus making the ventral part of the corpus the

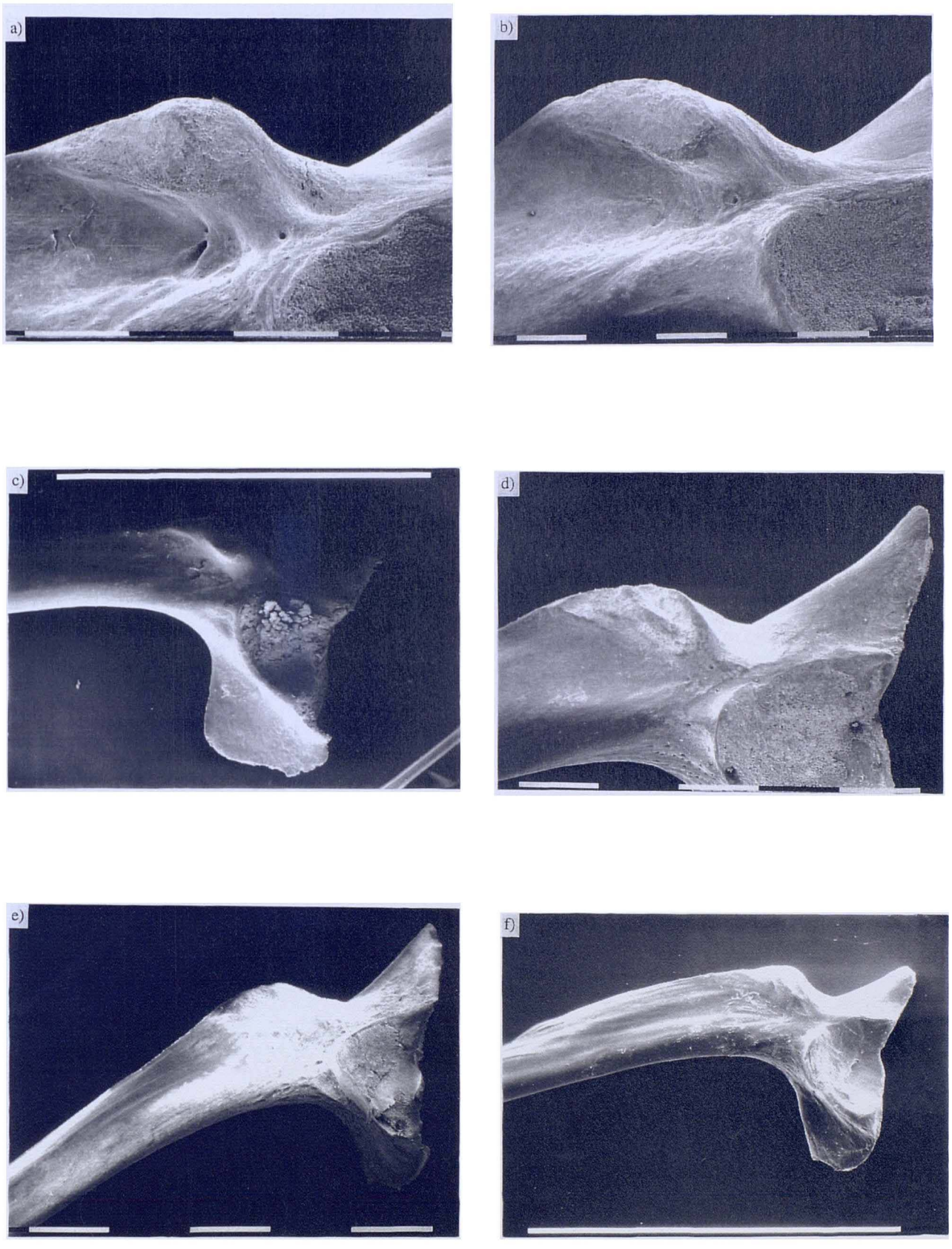


Figure 5.38:Left ilia (lateral view) of *R. temporaria*: a) detail of tuber superior, CGO 2/19; b) detail of tuber superior, CGO2/7; c) CGO 2/3; d) CGO 2/23; e) CGO 2/29 (juv.); f) CGO 2/5.

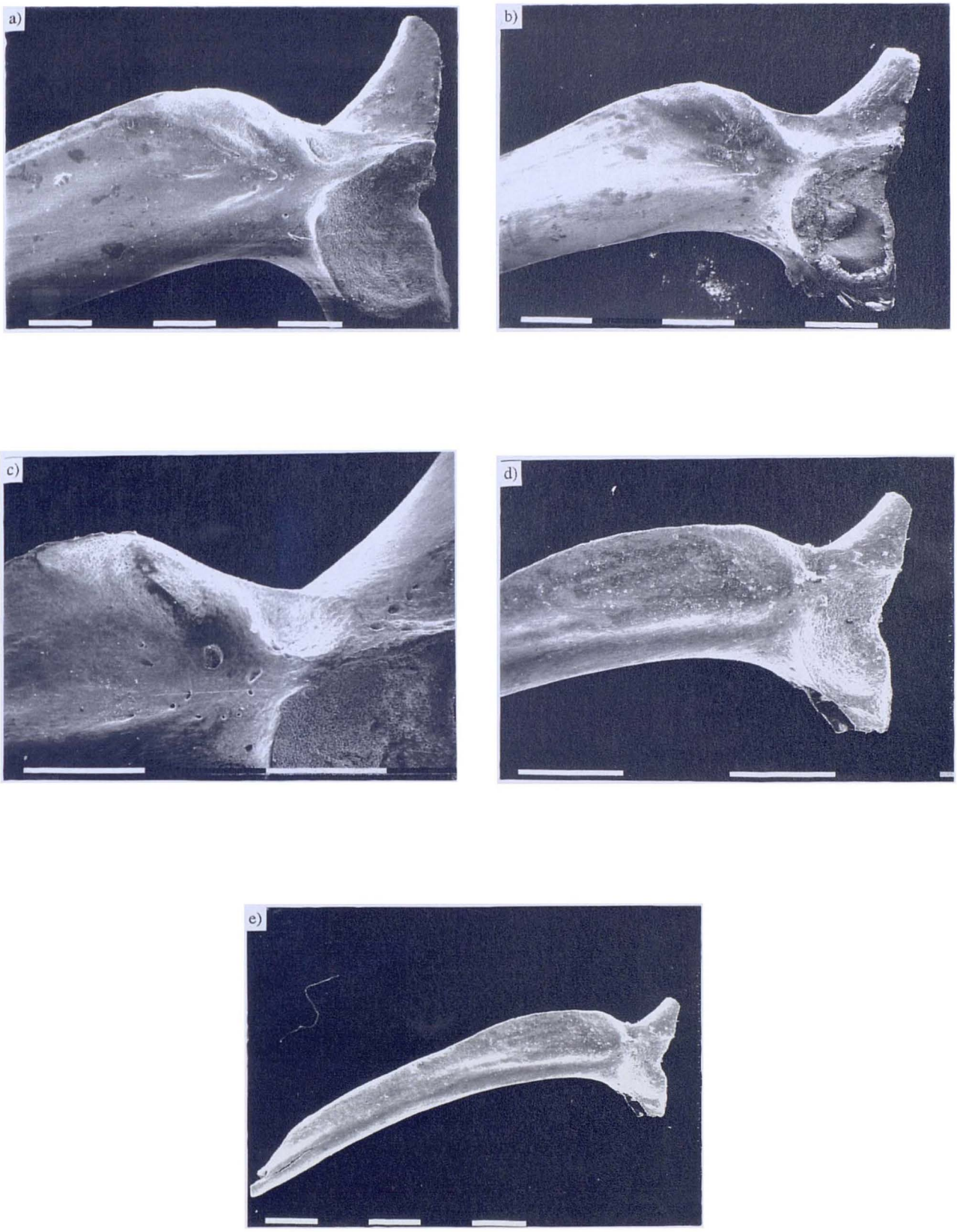


Figure 5.39 Left ilia (lateral view) of *R. arvalis*: a) C. Snell coll., 60mm; b) C. Snell coll., 42mm; c) detail of tuber and supra-acetabular fossa, C. Snell coll.; d) C. Snell coll. (juv.); e) C. Snell coll. (juv.).

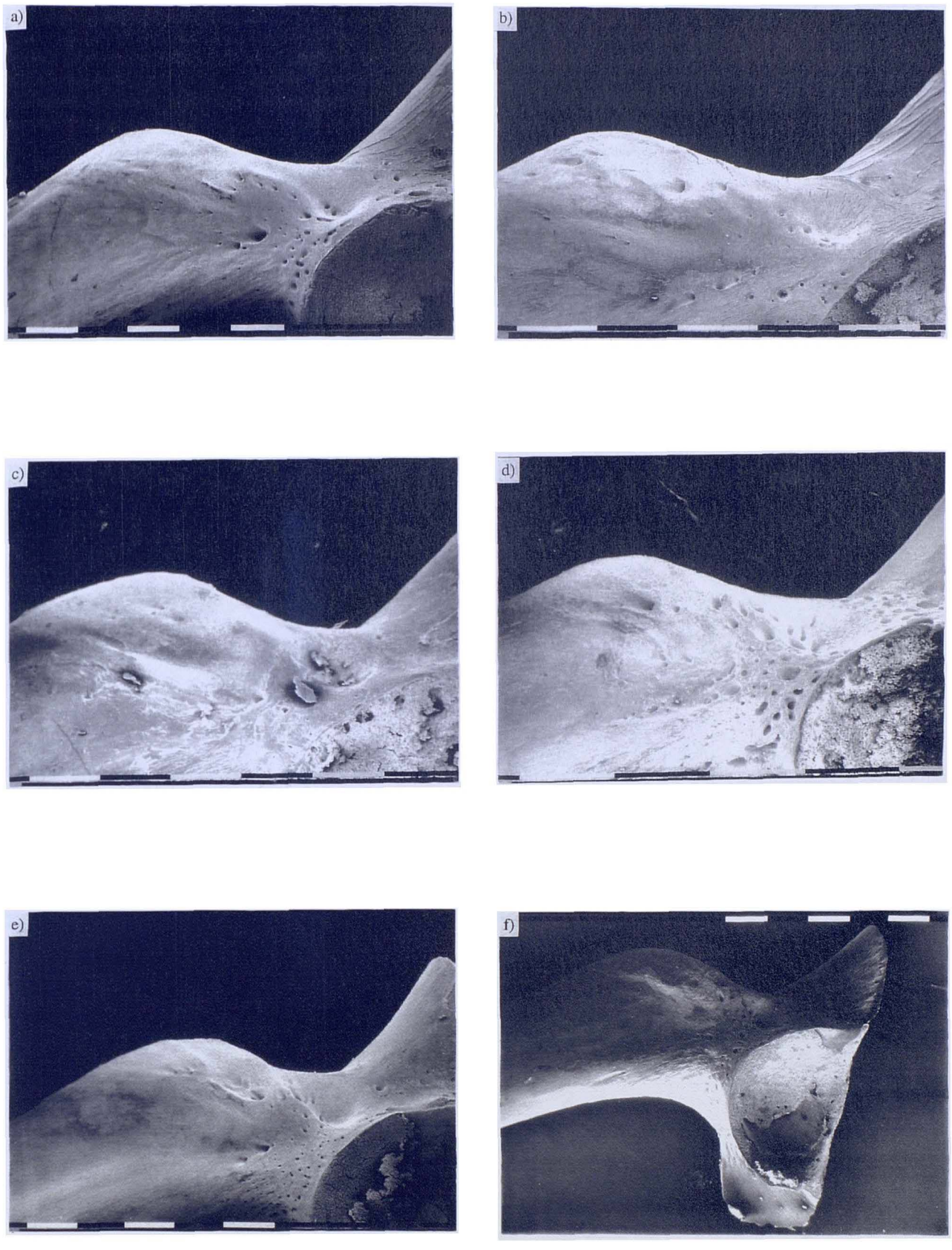
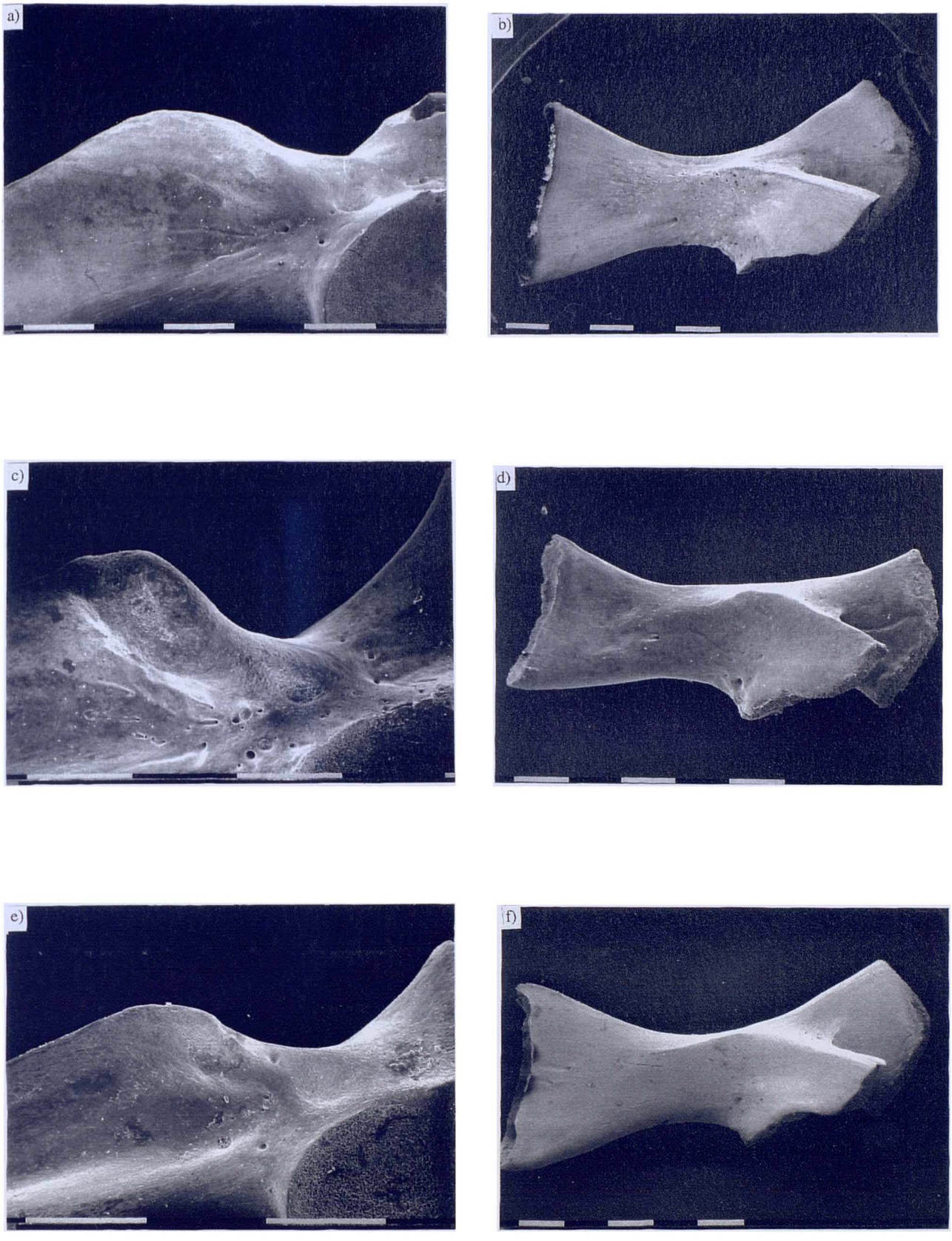


Figure 5.40.Left ilia (lateral view) of *R. ridibunda*: a) CGO 42/10; b) CGO 42/7; c) CGO 42/5; d) CGO 42/9; e) CGO 42/16; f) CGO 42/1.



Figue 5.41 : a) left ilium of *R. lessonae*, C. Snell coll., SE London specimen; b) left scapula of *R. ridibunda* (CGO 42/18); c) left ilium, J. Buckley coll., Norfolk specimen; d) left scapula of *R. lessonae*, J. Buckley coll., Norfolk specimen; e) left ilium, C. Snell coll., Swedish specimen; f) left scapula of *R. esculenta* (CGO 44/4).

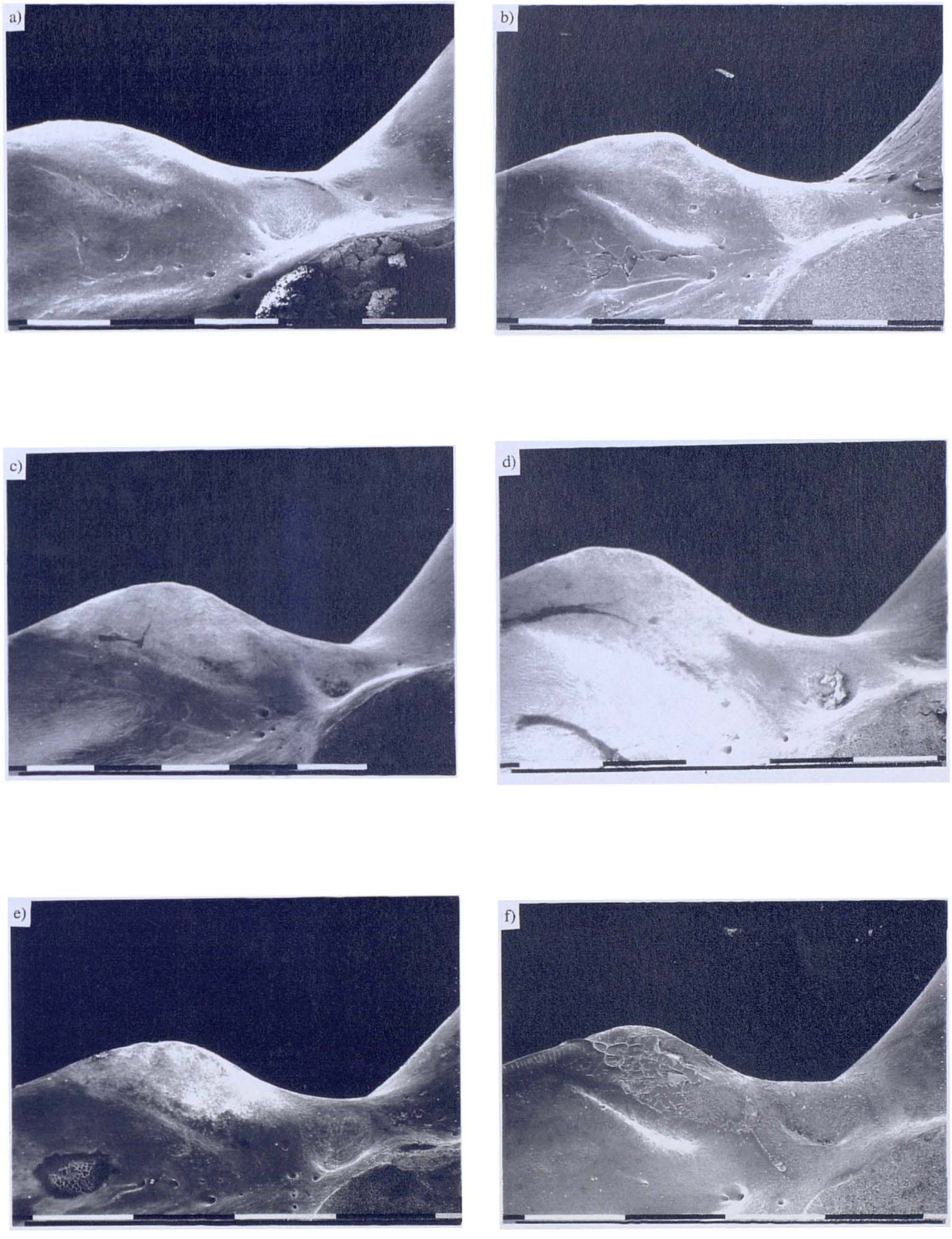


Figure 5.42: Left ilia (lateral view) of *R. esculenta*: a) CGO 44/7; b) CGO 44/5; c) CGO 44/3; d) CGO 44/4; e) CGO 44/10; f) CGO 44/9.

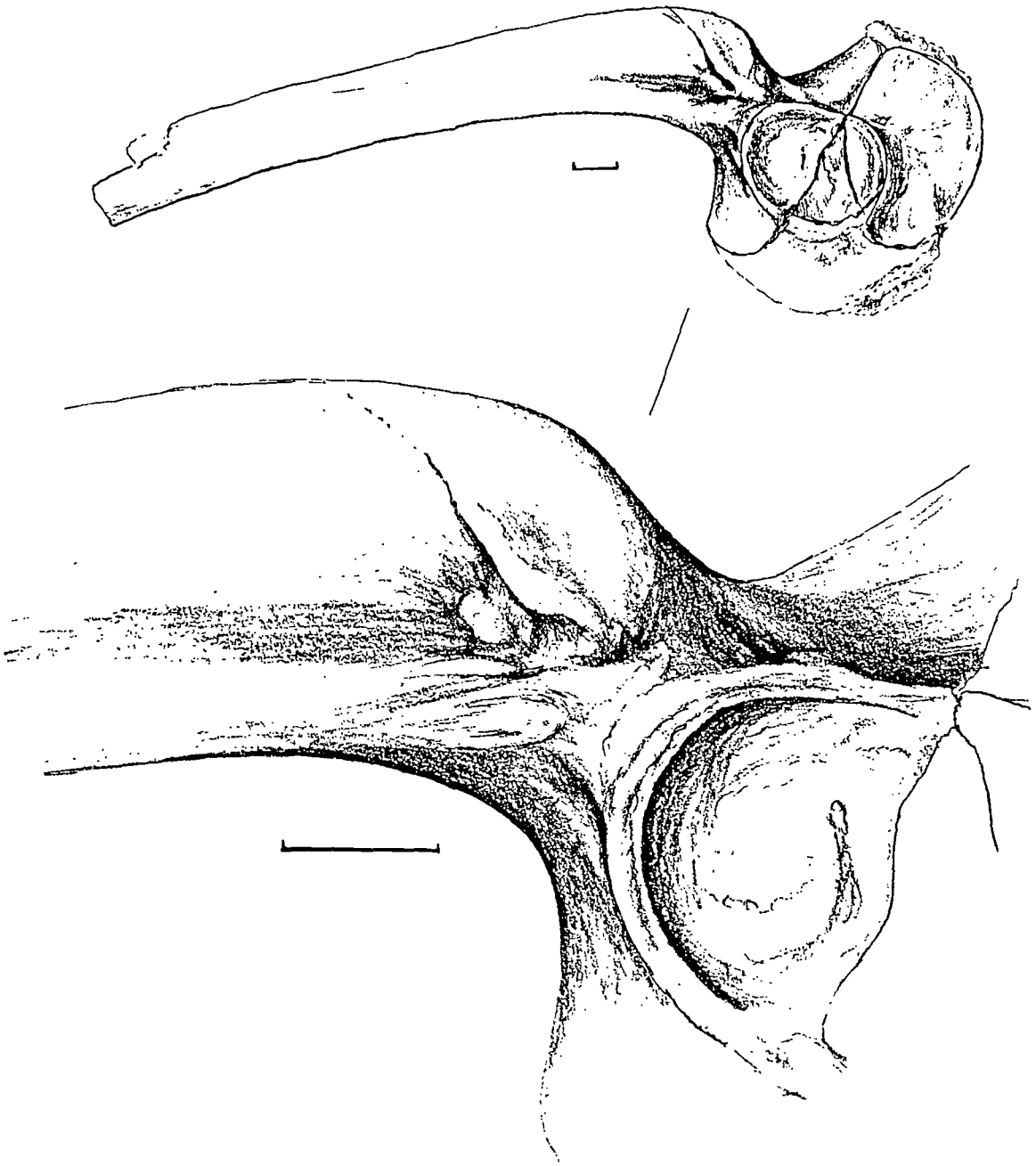


Figure 543: Left ilium of *R. ridibunda* (BMNH collection: BM 1976, 1697 6.8) (1mm scales).

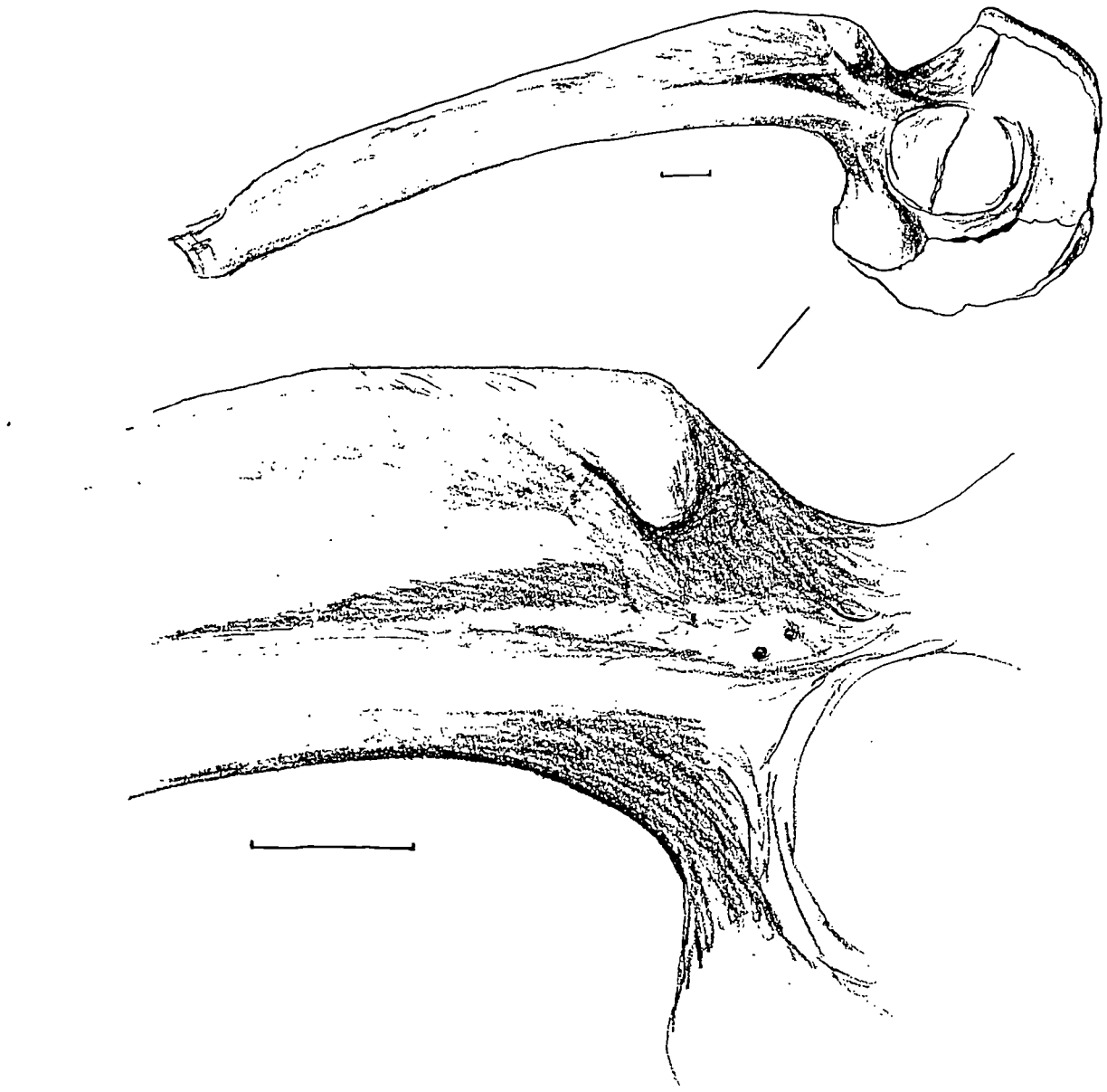


Figure 5.44: Left ilium of *R. lessonae* (BMNH collection: RR.1933.2.20.14 Camerano, Turin) (1mm scales).

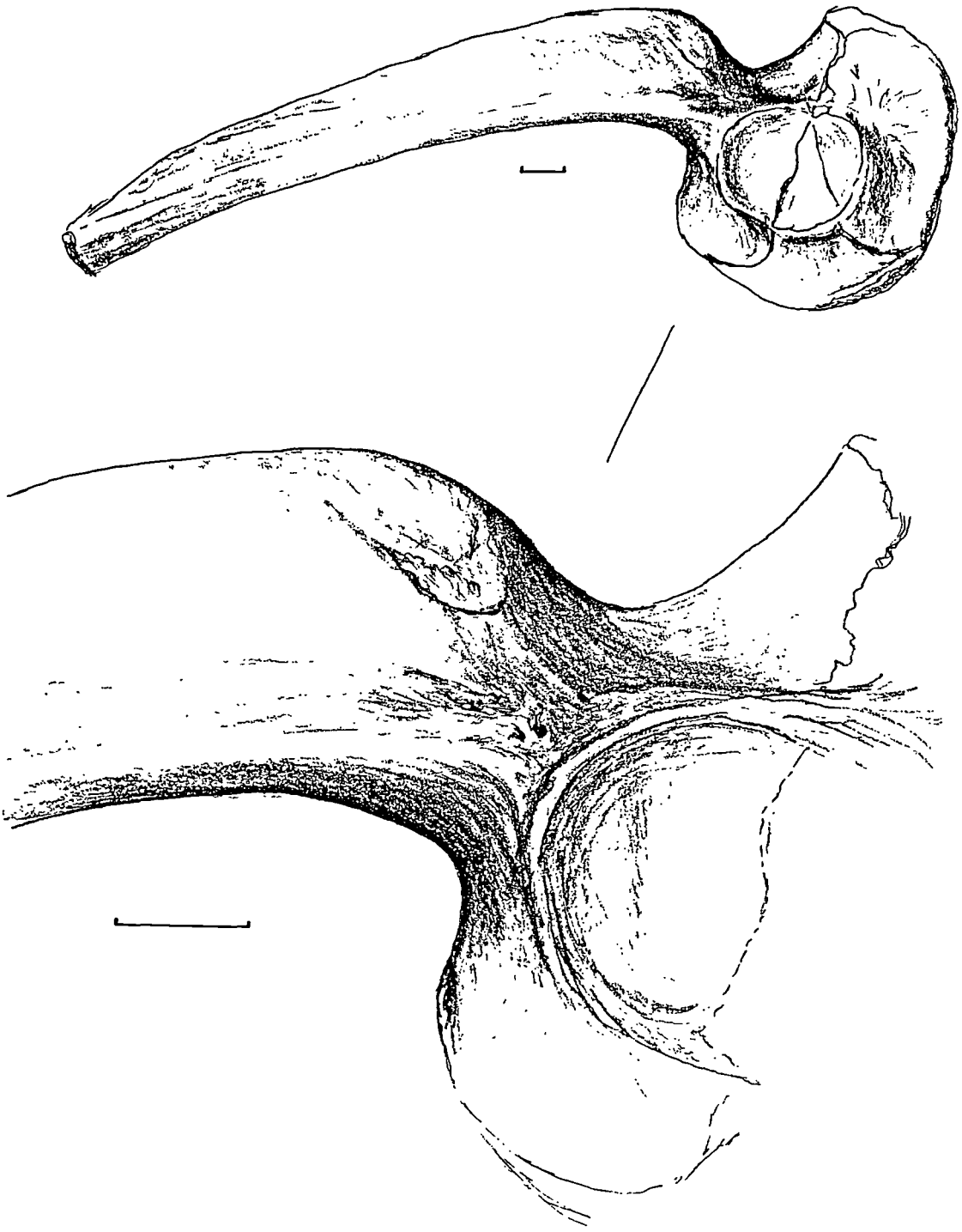


Figure 54 Left ilium of *R. esculenta* (BMNH collection: 97.6.3 (p39) Prater, Vienna) (1mm scales).

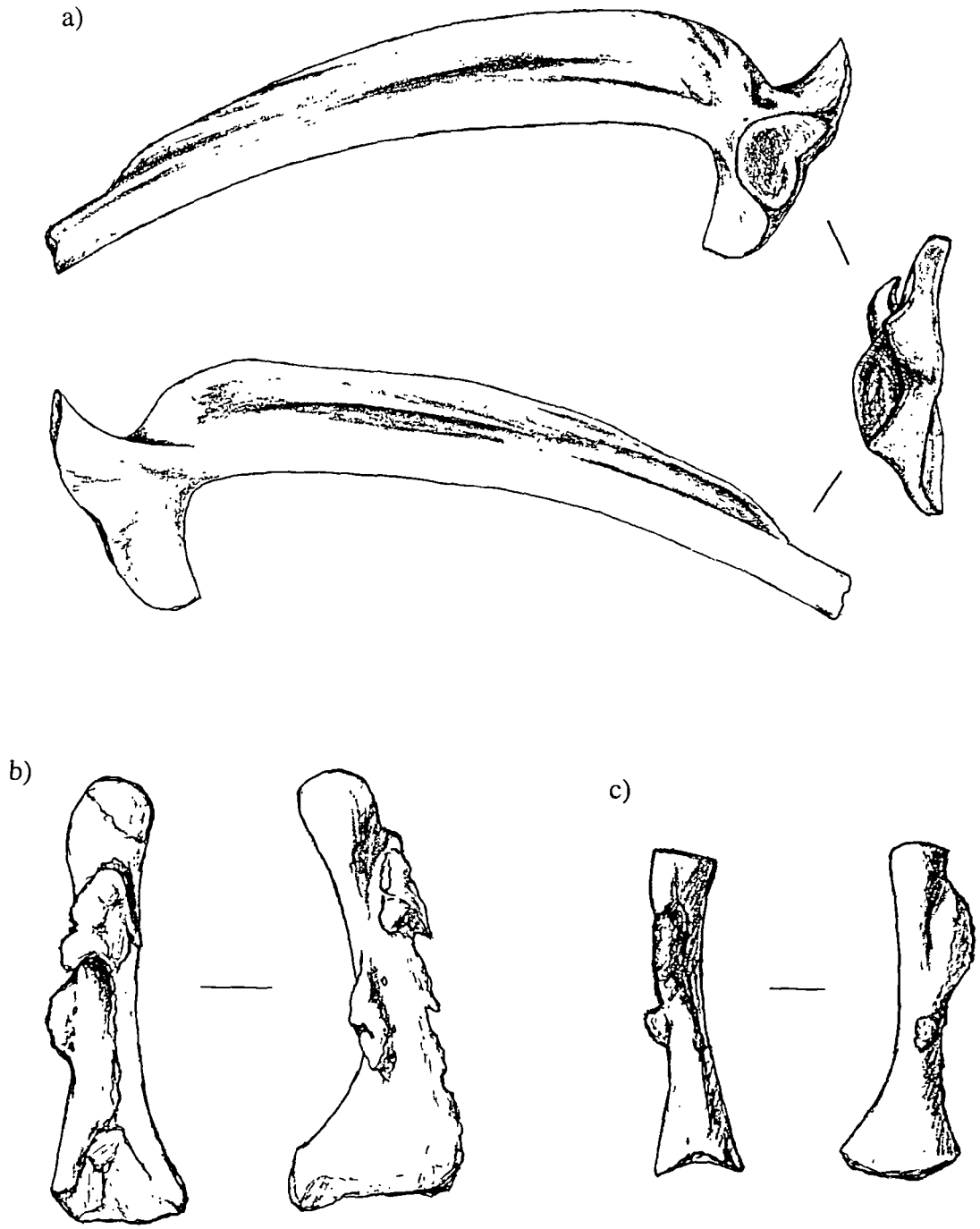


Figure 5.46: a) Left ilium of *R. dalmatina* (PAS collection: ZZsid448); b) male second digit metacarpal of *R. arvalis* (ZZsid67(1952)); c) male second digit metacarpal of *R. dalmatina* (ZZsid448).

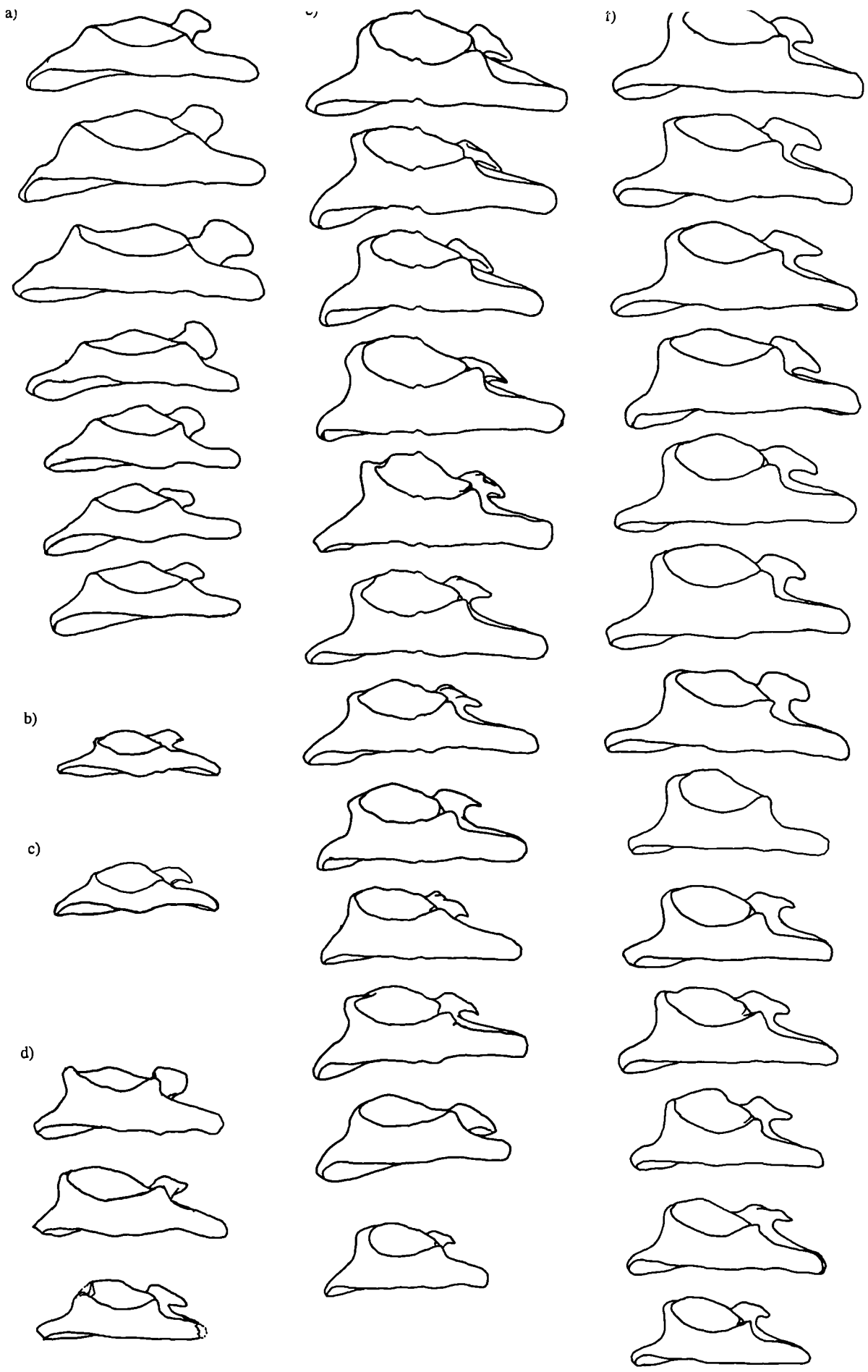


Figure 5.47: Junctura ilioischiadica of: a) *R. temporaria*; b) *R. arvalis*; c) *R. dalmatina*; d) *R. lessonae*; e) *R. ridibunda*; f) *R. esculenta*..

thickest. In brown frogs, the junctura is consistently more slender, with no great difference in thickness below dorsal and ventral acetabular walls. The medial part of the outline is also somewhat more sinuous. *R. arvalis* has a slightly thinner junctura than *R. temporaria*. According to Böhme (1977), the junctura of *R. dalmatina* is also very slender and the ilium is overall very similar to *R. arvalis*.

The tuber superior can be used fairly confidently to separate the green and brown frog groups, and in most cases, *R. temporaria* can be isolated. There is a high degree of variation in the ilium of *Rana*, but some typical forms may be isolated. In other cases, distinction is not possible, due to overlap and morphological ambiguity. It is also difficult to confidently define specific traits, as the taxonomic status of *Rana*, let alone its geographical variation, is incompletely understood. The relationship of ilial morphological variation to possible subspeciation, hybridisation or isolation in the past, is also unknown.

The tuber of green frogs is robust, with a thick posterior edge and shouldered apex. The margo dorsalis of the vexillum is also straighter in the green frogs than in *R. arvalis*, but this rarely survives intact in fossil specimens. In *R. ridibunda* and *esculenta*, the tuber has a clearly defined anterior border on its lateral side, radiating across the vexillum obliquely. This forms a flat lateral facet, protruding laterally from the vexillum, and approximately trapezoid in shape. This is relatively narrow in *R. ridibunda*, becoming wider and more flared in *R. esculenta*. The tuber is more tumid and bulges laterally in *R. lessonae*, without a clearly defined lateral facet. The posterior edge of the tuber is steeper and more sinuous in *R. lessonae*, and is relatively shallow-sloping in *R. ridibunda*. Some of the *R. esculenta* seen have a somewhat sinous posterior margin, but none are as laterally protrusive as the *R. lessonae* specimens seen. Böhme and Günther (1979) studied 318 recent specimens of green frogs and found that the tuber was positioned more closely to the acetabulum in *R. lessonae* than in *R. ridibunda*. However, as *R. esculenta* showed an intermediate position ranging between both parent species, the parameters of this character could not be defined clearly.

R. arvalis has a more gracile tuber than green frogs, tapering dorsally and grading smoothly into the vexillum. It is bulbous lower down, but becomes completely flat higher up. Younger specimens (e.g. Figure 5.39c, d) appear to have distinctly triangular facets. Other specimens (e.g. Figure 5.39a, b) have a more sculpted tuber, with imbricated ribs on the lateral face (cf. *R. a. wolterstorfii* of Böhme, 1977), but these ribs are not as pronounced as in *R .temporaria*. The vexillum is more arcuate in its outline than the green frogs, its posterior edge is not as steep, and its apex is not angular but smoothly rounded. According to Böhme (1977), the tuber and vexillum of *R. dalmatina* are similar to *R. arvalis*, but the vexillum is more medially curved. The tuber in *R. arvalis* generally has its posterior edge connected to the pars ascendens by a thin crista, enhanced by the deeply excavated supra-acetabular fossa (see Figure 5.39c). This is a fairly diagnostic feature, which seems to separate *R. arvalis* from similarly ribbed specimens of *R. temporaria*.

R. temporaria is the most variable species, and displays a range of forms in the tuber and

vexillum. Generally, the tuber is low and irregular, often laterally bulbous and sometimes with a ribbed lateral relief. Some specimens with bulbous tubers, have a deep fossa at the intersection of the tuber and the ala (e.g. Figure 5.38a). The vexillum is usually lower in height than the tuber apex, but occasional specimens have a continuously high vexillum (e.g. Figure 5.38f). The posterior edge of the tuber is steeper and more shouldered than in *R. arvalis*, and the supra-acetabular fossa is not usually deep.

Some juvenile specimens of *R. esculenta* (around 25mm snout-vent length) have ilia with a high vexillum, but lacking the fully developed tuber character of adults. The tuber is not laterally produced and is almost indistinguishable from the vexillum. In contrast, some fossil specimens of brown frog species have strongly ribbed tubers, even in minute specimens, and these seem to exhibit specific traits.

Urostyle

The urostyle is also known as the os coccygis, particularly in older literature (e.g. Gaupp, 1896). It takes the form of an elongate sub-cylindrical rod, with a thin dorsal blade (neural spine) formed from two laminae meeting dorsally. Sharing a trait which is characteristic of the whole vertebral column in anurans, its form is very variable in both *Rana* and *Bufo*, and separation of *B. bufo* from *Rana* can be difficult. Separation from other genera is easily done, on the basis of shape nad form. The dorsal edge is often irregular: dividing and coalescing along its length. There is a coccygeal canal on either side of the spine, towards its anterior end, entering obliquely and leading to the vertebral canal. The shape, size, position and even presence of these canals is very variable, and yields little diagnostic information even to generic level. The elongate rod of the corpus tapers slightly posteriorly, but has a variable cross-sectional shape. It is more flattened in *Rana* than in *Bufo*, and is more acutely curved laterally, so that the dorsal spine appears more tightly pinched at its base. Distinction from *B. calamita* and *viridis* is simple, but *B. bufo* is more difficult to separate. The shape of the articular cups (cotyles), which connect with the paired condyles of the sacrum, is generally rounded in *Rana*, but can be ovate. The cotyles of *B. calamita* are similarly rounded, but *B. calamita* and *viridis* are more vertically compressed, with elliptical cotyles. The dorsal spine is high in both genera, but perhaps higher in *Rana* than in *Bufo*. The apex is generally expanded into a boss which is very variable in shape and size. The shape of the vertebral canal opening below is correspondingly variable, but roughly triangular in both genera. The spine's anterior end can be vertical, or slope anteriorly or posteriorly. In the green frogs, it consistently slopes posteriorly, with a straight anterior edge in lateral view. In *R. temporaria* and *arvalis* the anterior end is almost vertical, but with an irregular, straight or concave edge in lateral view. In these species, this region is similar in shape to *Bufo*.

APPENDICULAR SKELETON

The humerus is sexually dimorphic, with males exhibiting features which can allow specific

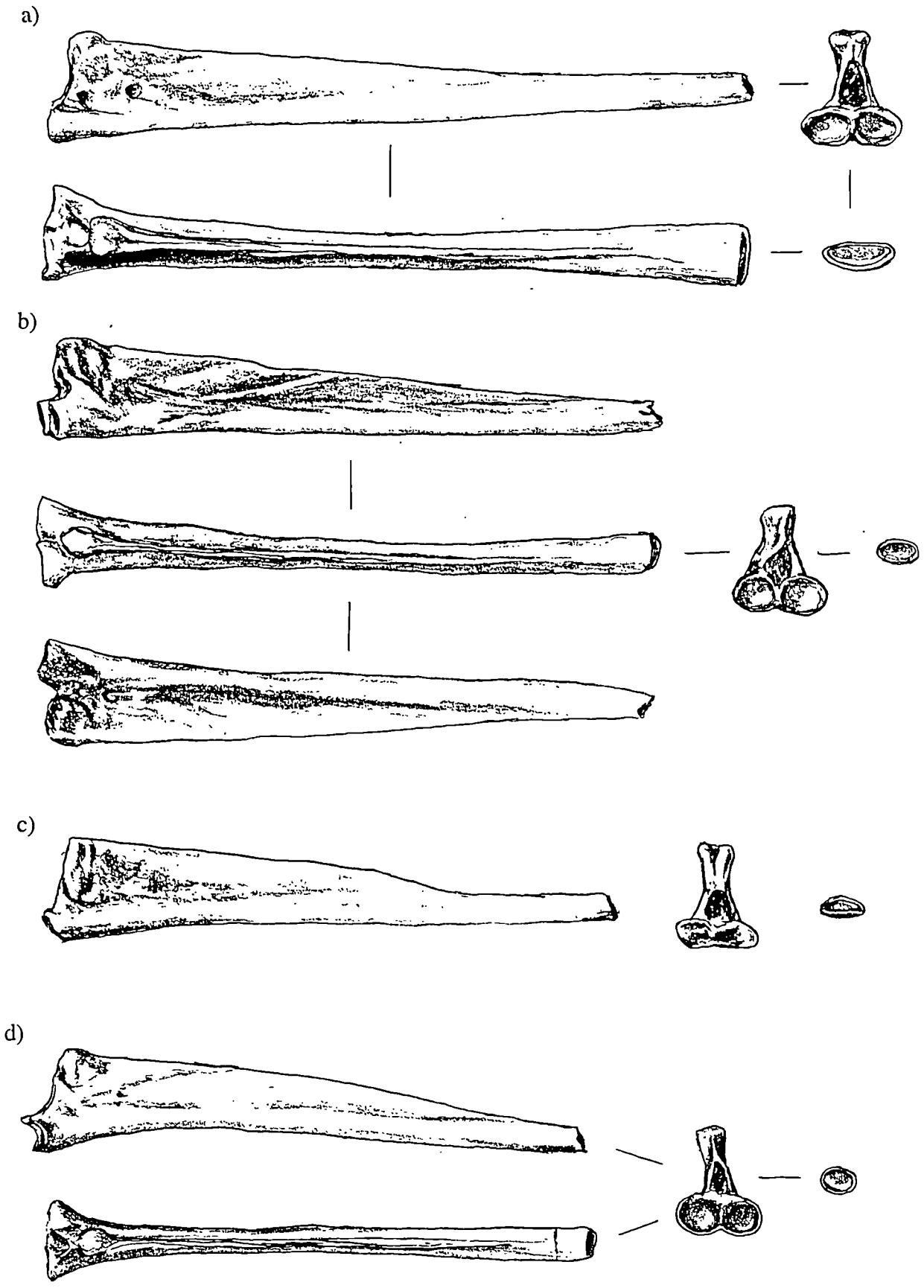


Figure 5.8: Urostyle of: a) *R. ridibunda* (BMNH: 33 (p39)); b) *R. ridibunda* (BMNH: BM 1976, 1697 6.8); c) *R. lessonae* (BMNH: RR.1933.2.20.14); d) *R. esculenta* (BMNH: 97.6.3.3 (p39)).

determination. This bone is commonly preserved as a subfossil. Though also found abundantly, often in fragmentary condition, the femora, tibiofibulae and radioulnae are as yet indistinguishable between species. It is likely that more detailed study of the femur and tibiofibula would allow distinction between green frogs and brown frogs. Length and diameter proportions, cristae and position of foramina may yet offer some distinction, but would require more detailed study. However, these elements can probably offer less information than other more diagnostic ones, and further effort might be better placed concentrating on those.

Humerus

The humerus is a sexually diagnostic bone, and male specimens are more useful in specific determination. In females, the only useful characteristic is in the shape of the lower shaft. In green frogs it is straighter in lateral view, and in brown frogs it has a greater curvature. In males, two flared ridges develop to accommodate the muscles required for prolonged amplexus. These are known as the crista medialis and crista lateralis (Ecker, 1889; Gaupp, 1896) and are best viewed in anterior or posterior view. Their strength is dependant on sexual and ontogenetic maturity, but their morphology is specifically diagnostic. Rage (1974) made identifications based on the humerus of *Rana*. The current work agrees that this is possible. In green frogs the medial crista is wide and broadly curved, whereas in the brown frogs, it is straighter and narrower, but reaches further up the humeral shaft. In the green frogs, the cristae appear smooth from posterior view, giving the humerus a flat posterior face. In *R. temporaria*, both the medial and lateral cristata are directed posteriorly and continue up the back of the shaft as sharp ridges, converging at the proximal epiphysis. In *R. arvalis*, only the medial crista is deflected backwards strongly, and continues up centre of the shaft as a single sharp posterior crista. The front of the humerus also develops a strong bladelike flange, extending from the upper part of the shaft. Ecker (1889) referred to this as the crista deltoidea, and Gaupp (1896) named it the crista ventralis. Here this is considered as the anterior side of the humerus.

Radioulnae

No diagnostic criteria have been found, though further study is probably waranted as these are some of the most abundantly preserved elements in subfossil environments. Owen (1990) found that radioulnae had little value for identification, after a biometric study of these elements in *R. temporaria* and *B. bufo*.

Tibiofibulae

This bone is one of the most commonly found elements in fossil assemblages. Its shape is an elongate cylinder, which widens and divides into two parallel cylinders at either end. The tibiofibula in *Rana* is long and slender, with a round diaphyseal cross-section. It lacks the sharp marginal cristata and the flattened cross-section found in *Bufo*. In *R. temporaria* and *R. arvalis*, the

tibiofibula is almost straight; in the green frogs it is noticeably curved. *R. lessonae* has much shorter tibiofibulae than the other species, corresponding to its shorter legs. *R. esculenta* is intermediate in size, but not conspicuously shorter than the brown frogs or *R. ridibunda*. *R. lessonae* has very robust tibiofibulae, with a markedly bowed shape, making it the most distinctive species.

Tibiale and Fibulare

These are difficult elements to isolate diagnostic criteria from, but there is a greater tendency towards ossification of the epiphyses in *R. temporaria* than in other species, and perhaps more so in the brown frogs than in the green frogs. The morphology of the ossified articulatory surfaces may offer some information.

Metapodials and phalanges

These are the bones of the hands, feet and toes, and are generally the elements of the anuran skeleton found in the greatest abundance as fossils. Their relative abundance reflects the the large number of them in the anuran skeleton. They are cylindrical (conical in the distal phalanges) and are easily preserved due to their rigidity. For most, their surface morphology is relatively featureless and their overall shape similar between species, and no distinct features have been found which would allow specific identification. These bones are recogniseably anuran when found as fossils, and in some cases can be identified to genus or species, but on the whole are relatively useless.

The first metacarpal in male ranid frogs is an exception. It always displays an irregularly-shaped, gnarled and contorted tuber (cristae nuptia) along much of its length, to which the nuptial pad muscles are attached. This bone is very distinctive in its surface morphology, and is easily separated from the same bone in other genera. It is also wider at its proximal end, and its proximal articulation is oblique. The tubers are very variable in their morphology. As might be expected, their development is strongly linked, primarily, to ontogenetic maturiy, and this may cause too much variation for specific determination to be possible. Consistent characters have not been isolated for each species.

5.10 Emydidae

(*Emys orbicularis*)

The shell skeleton of chelonians is so distinctive from other reptiles or amphibians, that it needs little description. The rest of the skeleton has not been recorded or considered as much in the literature, but some elements are also easily diagnosed. Isberg (1929) and Degerbøl and Krog (1951) described numerous very well preserved *E. orbicularis* specimens from Holocene peat deposits. The series of photographs in the latter publication clearly show the distinctive character of *Emys* shell, and to some degree the potential variation in its shape. E.T. Newton (1879) also gave an excellent illustration of the Mundesley specimen (see Figure 3.10). Holman (1995c) considered the comparative shell osteology of *E. orbicularis* and *Mauremys caspica leprosa*, and demonstrated that differences were sufficient to separate these species. Mlynarski (1976) reviewed all systematically described European chelonian fossil records, though only with a brief discussion of *E. orbicularis*.

Whereas Stuart (1979) considered it unlikely that any species other than *E. orbicularis* would be found in the British Pleistocene, Holman (1995) believed this to be a distinct likelihood. However, no other chelonian species has a range which even approaches northern Europe. It is therefore considered very unlikely that species such as *M. leprosa* may have reached Britain. Thus, it is assumed that only *E. orbicularis* has appeared in the British Quaternary fossil record.

One specimen has been obtained (CGO 30/1), as well as two additional complete carapaces and plastra, loaned by G.R. Coope (CGO 30/2, 30/3). The only detailed osteological description of *E. orbicularis* was given by Bojanus (1819-1821) who illustrated its skeleton in detail. The lack of recent osteological descriptions for *E. orbicularis* is perhaps not surprising, as its osteology has apparently been considered so distinct that such descriptions are not necessary, and that illustrations are sufficient. Romer (1956) described all aspects of the chelonian skeleton, and some internal skeletal elements of other species are illustrated there. Almost all *E. orbicularis* fossil records are based on carapaceal and plastral remains. Description of the rest of the skeleton will be brief. Osteological terminology generally follows Romer (1956).

CRANIAL BONES

The chelonian skull is highly modified, with a narrow facial region and a greatly broadened posterior region (Romer, 1956). Individual elements will not be described here. It is not known how regularly they appear (unidentified) in fossil assemblages.

VERTEBRAE

There are fewer vertebrae in chelonians than in other reptiles (Saunders *et al*, 1969). The atlas is in three parts, fitting around the anteriorly produced odontoid process of the second (axis) cervical vertebra, as in the lizards and snakes. The other six cervical vertebrae are large, with very

produced zygapophyses. The neural spine is reduced to a low ridge, but there is a prominent and sharp ventral spine. The ten trunk vertebprae are joined to the carapace, are weakly built and can only be detached incomplete. The two sacral vertebrae are not fused to the carapace, and have ribs which articulate with the ilia. There are a number of caudal vertebrae which diminish rapidly in size.

CARAPACE AND PLASTRON

The carapace and plastron are solid bony units which form the outer body shell of all chelonians. Figure 5.49 shows the carapace and plastron of *E. orbicularis*. The carapace in *E. orbicularis* consists of forty-nine separate bones which are joined closely to form one unit. The peripheral edge is smooth and thickened, but all internal edges have a sharply irregular profile which allows them to interlock very tightly. The plastron consists of nine bones and fits together in the same way. There is some variation in shape amongst specimens, but the arrangement and shapes of individual bones is diagnostically constant. Both units are covered with a series of hard cutaneous scutes. These leave a network of deep grooves in the surface of many of the individual bones. The external arrangement of the scutes does not reflect the internal arrangement of carapaceal and plastral elements.

The anterior end of the carapace is formed by the nuchal bone, behind which there are seven small, roughly hexagonal neural plates. The posteriormost tip of the carapace is formed by the pygal bone. Radiating from the neurals, there are eight elongate pleurals (also known as costals) on each side. The curved edges of the carapace are formed by a row of eleven peripherals on each side. The first peripherals join the nuchal at the anterior end, and the eleventh peripherals join with the two posteriormost pygals. The individual bones may be found disarticulated in fossil assemblages, but often remain attached to at least one or two other elements.

The anterior end of the plastron is formed by an epiplastron on each side, behind which are the two large hyoplastra. These four bones enclose the roughly hexagonal entoplastron. This anterior half of the plastron hinges with the posterior half which is formed by four large plates. The paired hypolastra are rectagonal, with a sharp dorsal projection on their lateral borders. This is directed posteriorly and joins the carapace above, in the living animal. The posteriormost part of the plastron is formed by a subtriangular xiphiplastron on each side: the largest elements in the whole shell.

The external sculpture of the shell is rough and pitted, but the internal sides are smooth. The internal morphology of the bones also reflects the attachment of muscles and the internal skeleton, and can help identify the position of an isolated element. Comparison of fossil specimens with comparative material, or with Figure 3.10 should allow fairly simple recognition of each element.

PECTORAL GIRDLE

The pectoral girdle is formed by a distinctive L-shaped scapula and a spatulate coracoid. These join

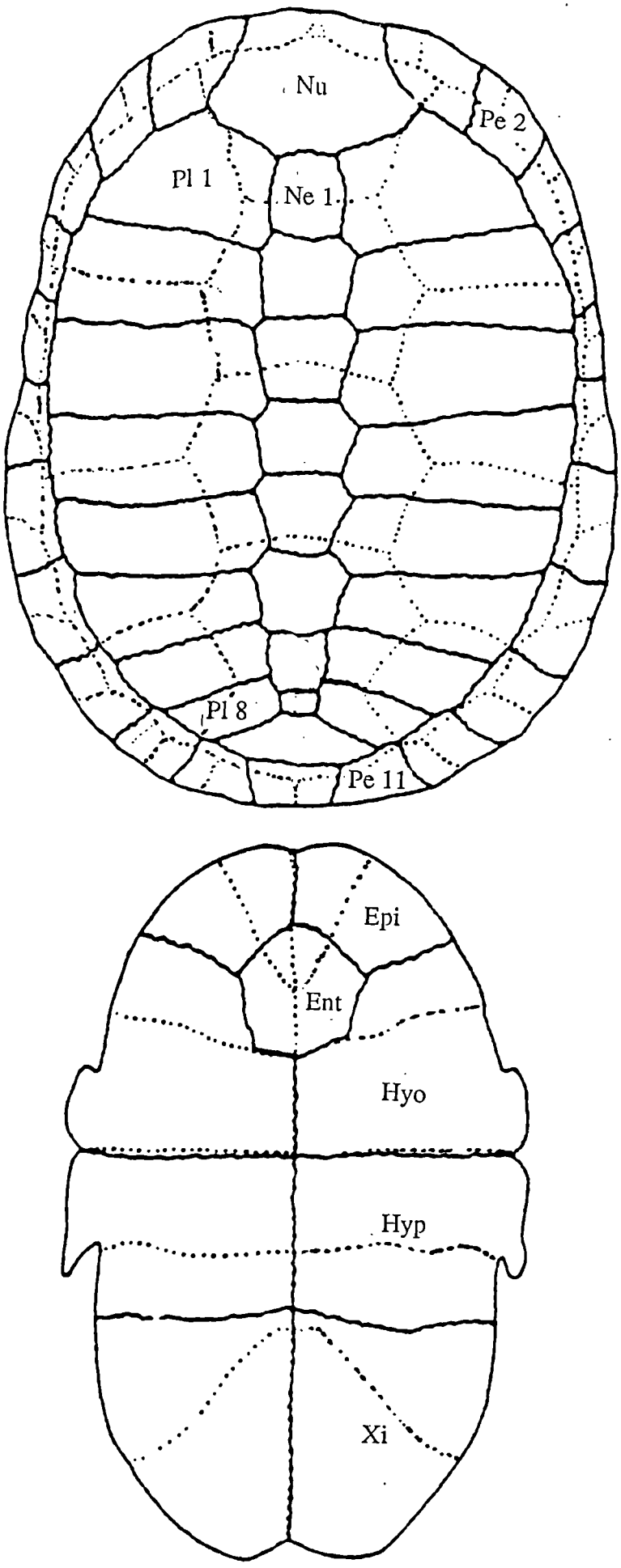


Figure 5.9 Carapace (dorsal view) and plastron (ventral view) of *E. orbicularis* (modified from Stuart, 1979). Key: Nu - nuchal; ne - neurals; Pl - pleurals; Pe - peripherals; Ent - entoplastron; Epi - epiplastron; Hyo - hyoplastron; Hyp - hypoplastron; Xi - xiphiplastron.

to form a tri-radiate strucutre of which the scapula extends dorsally to join the carapace, and the coracoid's lower branch extends ventromedially to the plastron (Saunders *et al*, 1969). At their proximal ends, both bones are excavated to form the glenoid fossa, for articulation with the humerus.

PELVIC GIRDLE

The pelvic girdle consists of an ilium, ischium and pubis on each side. These are fused at their proximal ends, forming the acetabular fossa to receive the femur. The robust ilia widen, distally, into flared blades which join the seventh pleurals of the carapace, and the sacral ribs. The ischia and pubes extend as widely flared plates and unite medially at the pubic and ischiadic symphyses. This forms a large fenestra on each side, known as the pubo-ischiadic foramen or thyroid fenestra (Saunders *et al*, 1969). The ischia have a robust posterolateral process which joins the plastron below. The pubes, which are anterior to the ischia and situated below the ilia, each have a narrower process which connect with the plastron also.

APPENDICULAR SKELETON

The humeri and femora are similarly shaped, and both have a curved shaft, ending distally with flared ridges, posteriorly directed on both sides. The rounded articular surface is positioned anteroventrally on the distal tip. The proximal end is wide in each, and the lower shaft is very constricted, before widening towards the distal articulation. It is very unlikely that these elements in *E. orbicularis* could be confused with any other animals.

The metapodials and phalanges are short and robust. The proximal end is wide and has a deeply excavated semicylindrical articular hollow. The anterior end is cylindrical, as in mammals, and these elements could be overlooked in fossil assemblages.

5.11 Lacertidae

(Lacerta viridis, Lacerta agilis, Lacerta vivipara, Podarcis muralis)

The Lacertidae have not been well described osteologically, a problem common to all lizard groups (Estes, 1983), and this is a relatively unworked field. The European lacertids are notoriously difficult to identify as living animals and it is likely that they are also osteologically very similar. From the three species for which comparative material has been studied, this is indeed true. From their distributions, most European species could be excluded as unlikely British Quaternary immigrants, and only four species *L. viridis, L. agilis, L. vivipara* and *P. muralis* are considered.

Smith (1969) provided an illustration of a *L. agilis* skull, which shows the typical lacertid form, and its composite elements. Romer (1956) discussed the osteology of lacertids, in relation to other reptile groups, and Estes (1983) considered all existing fossil records of the lacertids. Due to the observed similarity between the osteological characters for small lacertids, it appears that any identifications of such material from the British Pleistocene must involve at least some uncertainty. Description of material as "indistinguishable from" is unfortunately insufficient to make a confident identification to genus or species. Diagnosis as "cf. species" would be more appropriate, but it must be borne in mind that intraspecific variability has not been studied. Peters (1977) gave firm identifications of *L. agilis* and *L. vivipara* from a Holocene site in Germany, and it appears from the current studies that diagnosis of large lacertids is relatively easy.

The descriptions below are based on one specimen each of *L. agilis* (CGO 18/1, snout-vent length 70mm), *L. vivipara* (CGO 41/1, snout-vent length 46mm) and *P. muralis* (CGO 45/1, snout vent length 60mm). It would have been preferable to study a number of specimens for each species, but this was not possible. No specimens were collected for *L. viridis*, but a single specimen (Ref. no. MNCN 16504/16506) was studied at the MNCN. Osteological terminology follows that of Estes (1983), and Pratt (1946) where appropriate.

CRANIAL BONES

The cranial bones in all three species are superficially very similar, and probably the best guide to determination is relative size. Of the four species studied, all cranial bones of *L. viridis* are the largest, *L. agilis* is smaller, *P. muralis* is intermediate, and *L. vivipara* is the smallest. Figure 5.50a shows the form of the lacertid skull in *L. viridis*. As fossil lizard cranial bones are less commonly found than vertebrae, the problem of identification is alleviated somewhat.

Maxillae and dentaries

In all species, each tooth has three apices (cf. shark teeth), the middle one being much higher. The maxillae of *L. viridis* are easily distinguishable as they have a rugose external sculpture. The dentaries have five external foramina. Three are positioned anteriorly, two are placed in the middle section. The anterior tip of each tooth is sharp, but the posterior tip is not as prominent as in the

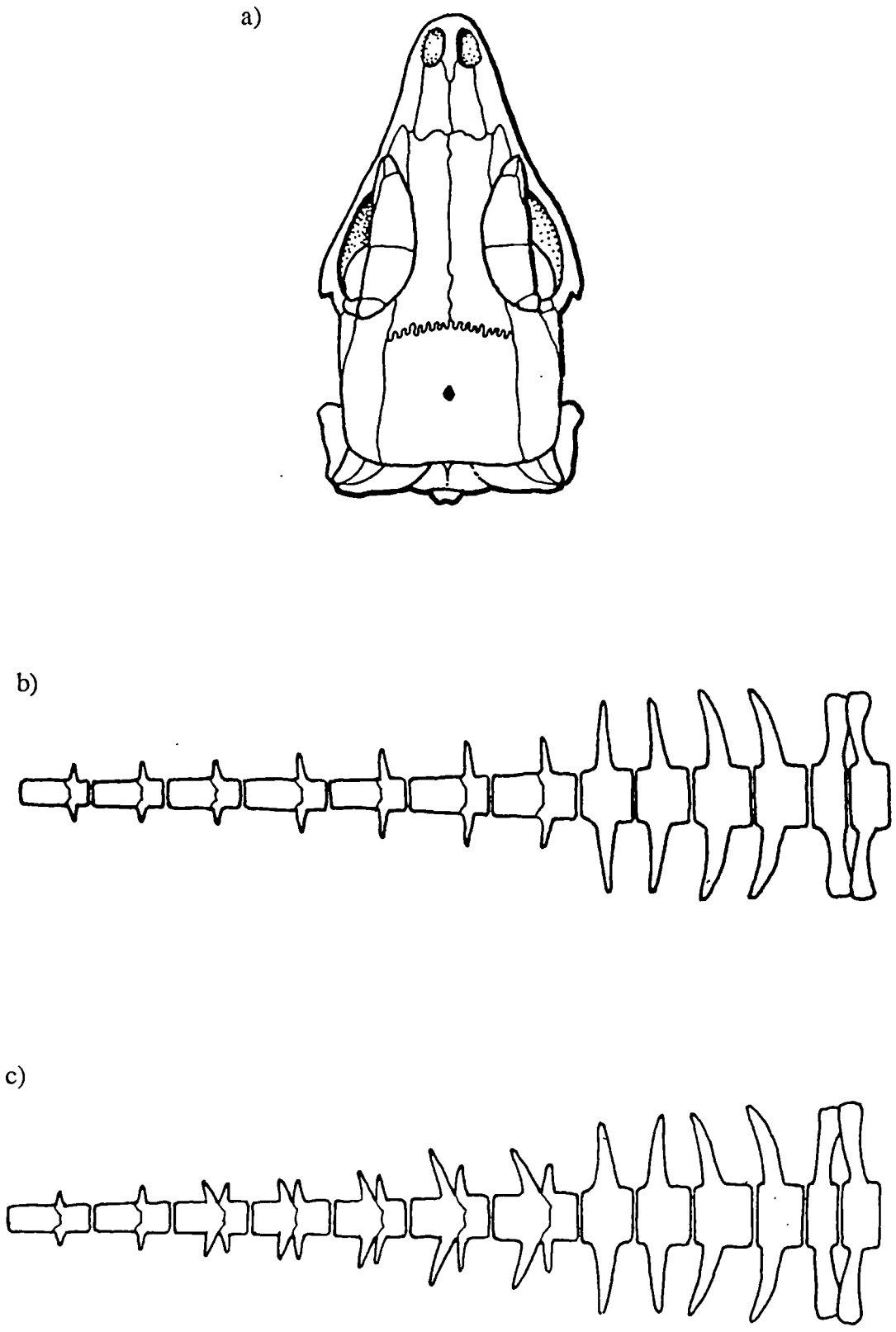


Figure 5.50: Parts of the lacertid skeleton: a) cranium of *L. viridis* in dorsal view; b) stylised sacral, postsacral and caudal vertebrae of *L. vivipara*; c) stylised sacral, postsacral and caudal vertebrae of *P. muralis* (after Arnold and Burton, 1978).

other species. The maxillae of *L. agilis, L. vivipara* and *P. muralis* are very similar in shape, and each has seventeen teeth, compared with twenty-two in *L. viridis*. The dentaries and other elements are difficult to distinguish morphologically, and no diagnostic criteria have been isolated. The teeth in the *L. agilis* and *P. muralis* specimens are noticeably less pointed than in the *L. vivipara* specimen.

VERTEBRAE

Vertebrae of *L. viridis* are immediately recogniseable by their larger size and general robust form. The vertebrae of *L. agilis* are easily distinguished from *L. vivipara* and *P. muralis*, on the basis of morphology. *P. muralis* can be distinguished from *L. vivipara*, but the differences are subtle. Vertebrae are probably the most useful elements for diagnosis of these species, not least because of their more regular occurrence in fossil assemblages.

Cervical vertebrae

The atlas consists of three parts, and the axis has a long odontoid peg, as in the snakes and chelonians. There are another five vertebrae which are noticeably shorter than the trunk vertebrae and could be considered as cervical. They apparently also bear ribs. These have short centra and steeply sloping neural spines. The neural spine is markedly longer and more produced in *L. agilis*, reaching posteriorly beyond the postzygapophyses. *P. muralis* has larger vertebrae than *L. vivipara*, but their less produced neural spine is a better guide. *L. viridis* has a broad, robust spine which is almost vertically directed, and connected by a sharp crest to the anterior neural arch (Figure 5.54b).

Trunk vertebrae

See Figures 5.51a-d, 5.52a-d, 5.53a,c ad 5.54a. Trunk vertebrae are relatively longer than the cervicals, and bear ribs attached to bulbous lateral articulations, at the anterior end of the centrum. Interestingly, there appear to be only fourteen in *L. agilis*, but nineteen in *L. vivipara*. The overall size of these vertebrae is noticeably greater in *L. viridis* than in the smaller species. Vertebrae are generally more elongate in *L. agilis* than in the small species. A typical centrum length was measured to be 3.0mm in *L. viridis* and 2.1mm in *L. agilis*, compared to 1.9mm in *P. muralis* and 1.6mm in *L. vivipara*. Trunk vertebrae of *L. vivipara* are much more compact, and not very much wider than they are long. *P. muralis* trunk vertebrae are of the same proportions as *L. vivipara*. Their underside is generally rounded, but the base of the centrum is more constricted in *P. muralis* than in *L. vivipara*. In *L. agilis* there can be a distinct haemal keel, sometimes divided into two ridges. In *L. viridis*, the centrum is pinched ventrolaterally.

The neural spine is the most useful diagnostic feature, and in *L. viridis* allows immediate diagnosis. In *L. viridis*, there is a long, broad-tipped dorsal spine, connected by a sharp, high crest to the anterior neural arch. The spine is much higher and more dorsally directed than in the other

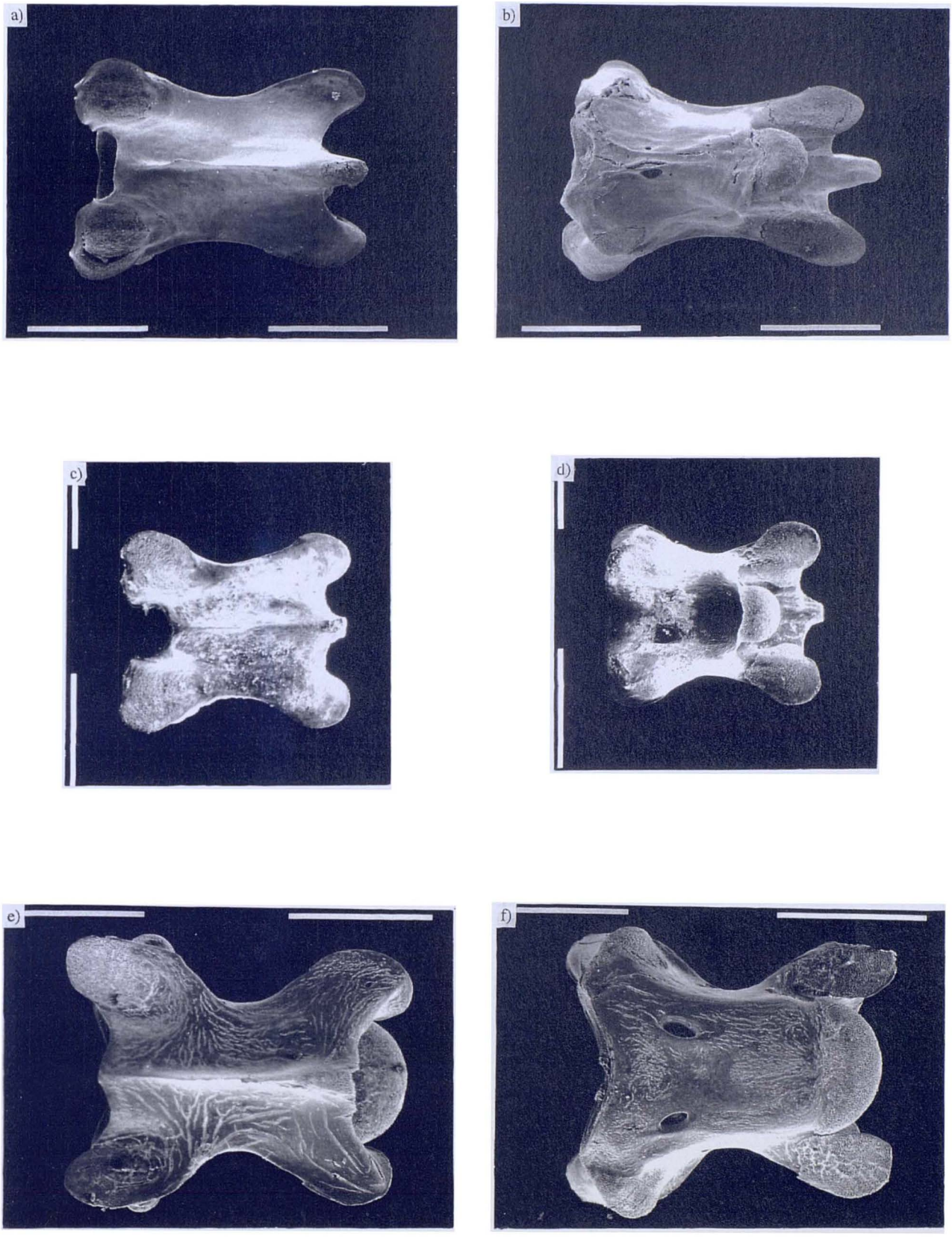


Figure 5.51. Trunk vertebra of: a) *L. agilis* (CGO 18/1), dorsal view; b) *L. agilis* (CGO 18/1), ventral view; c) *L. vivipara* (CGO 41/1), dorsal view; d) *L. vivipara* (CGO 41/1), ventral view; e) *A. fragilis* (CGO 16/1), dorsal view; f) *A. fragilis* (CGO 16/1), ventral view.

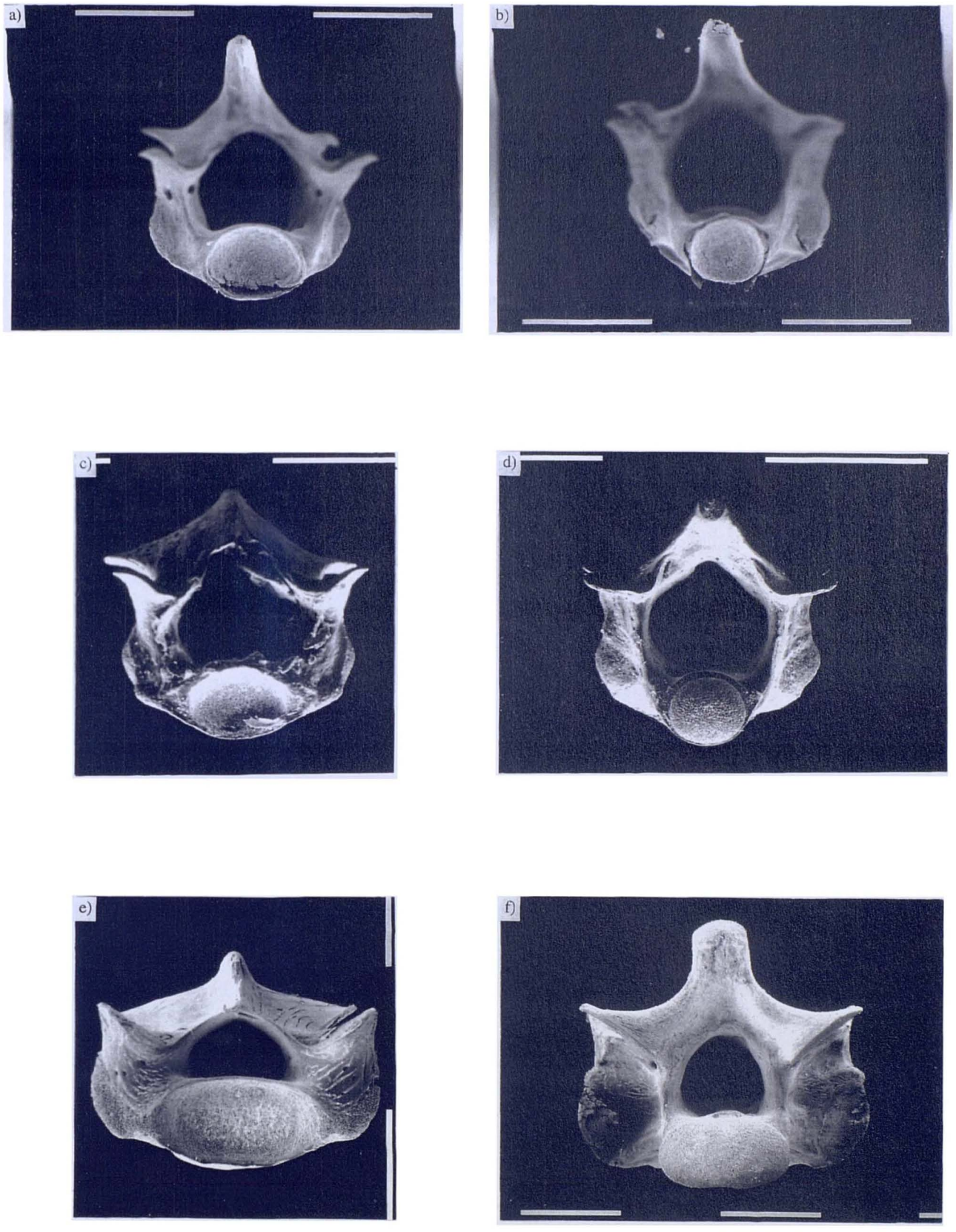


Figure 5.52:Trunk vertebra of: a) *L. agilis* (CGO 18/1), anterior view; b) *L. agilis* (CGO 18/1), posterior view; c) *L. vivipara* (CGO 41/1), anterior view; d) *L. vivipara* (CGO 41/1), posterior view; e) *A. fragilis* (CGO 16/1), anterior view; f) *A. fragilis* (CGO 16/1), posterior view.

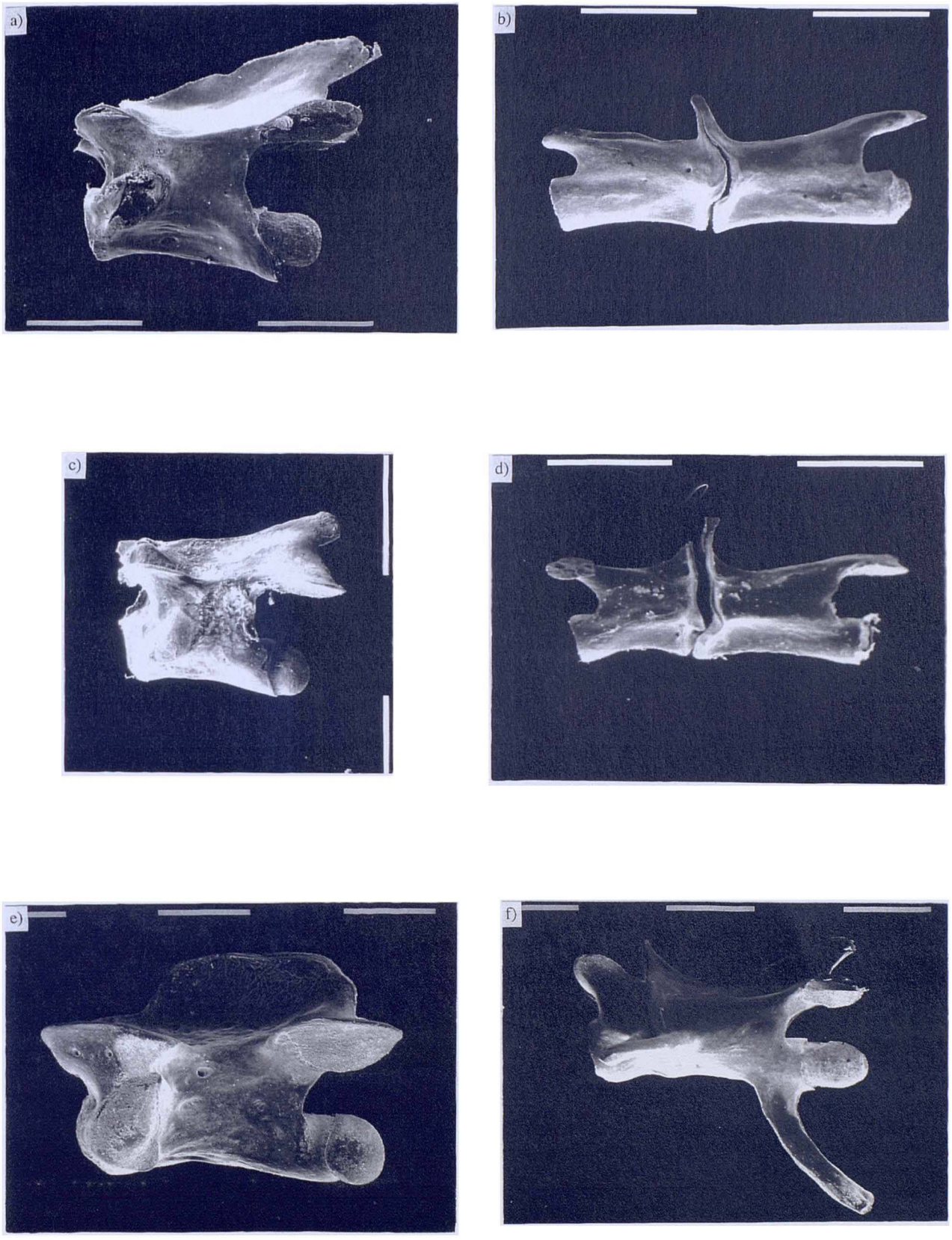


Figure 5.53.Left lateral view of: a) trunk vertebra of *L. agilis* (CGO 18/1); b) caudal vertebra of *L. agilis* (CGO 18/1); c) trunk vertebra of *L. vivipara* (CGO 41/1); d) caudal vertebra of *L. vivipara* (CGO 41/1); e) trunk vertebra of *A. fragilis* (CGO 16/4); f) caudal vertebra of *A. fragilis* (CGO 16/5).

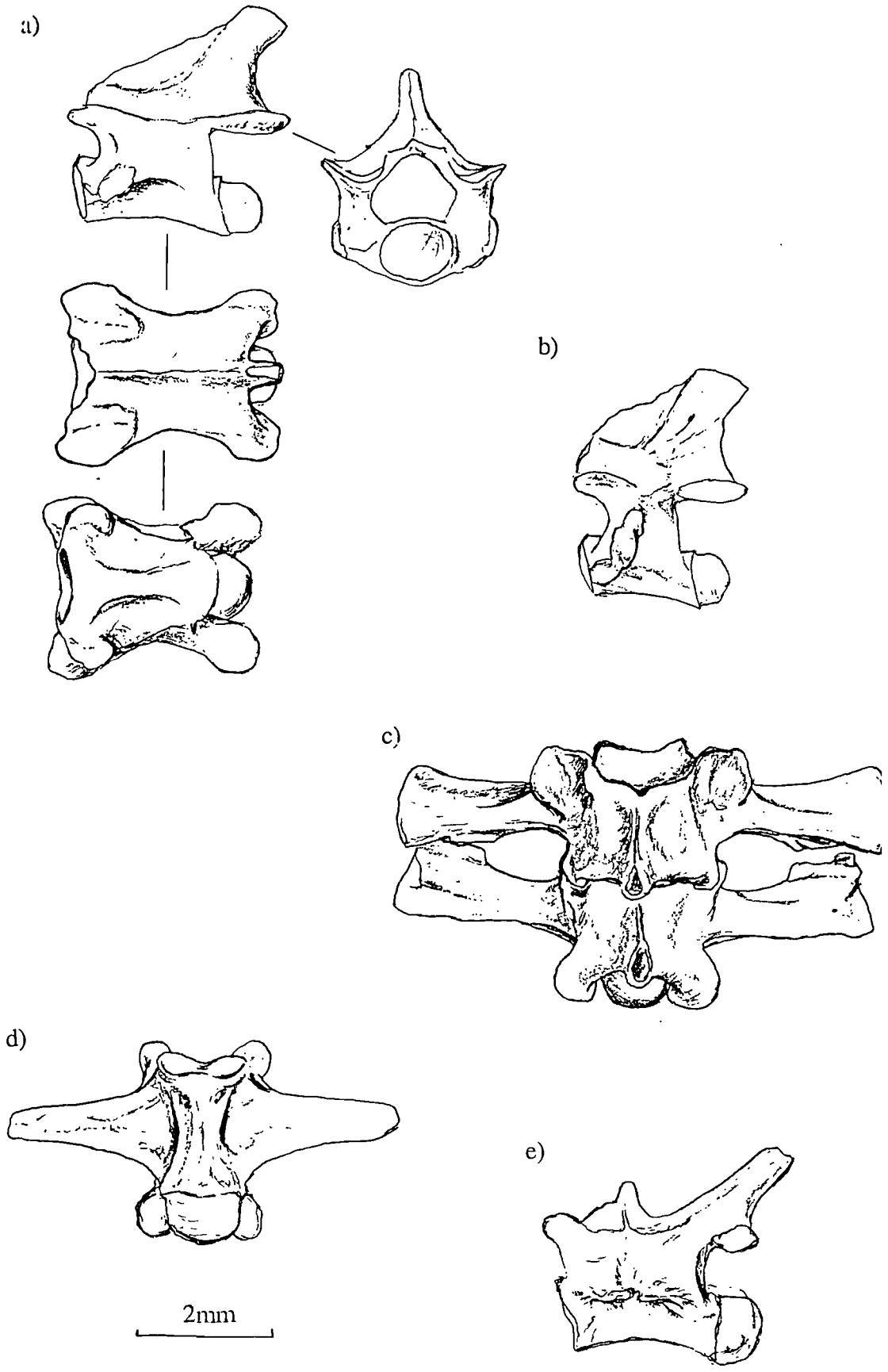


Figure 5.54: *L. viridis* (MNCN 16504, Bulgarian specimen): a) trunk (eighth) vertebra; b) cervical vertebra, left lateral view; c) 'presacrum' and sacrum, dorsal view; d) third post-sacral vertebra, ventral view; e) first caudal vertebra, left lateral view.

species, and in dorsal view only just reaches past the posterior condyle of the centrum. In the other species, the crest begins as a low, very thin blade anteriorly, but projects posterodorsally into a prominent spine. In *L. agilis* this is more gracile, with a higher blade, and its tip reaches posteriorly beyond the postzygapophyseal facets. In *L. vivipara* and *P. muralis*, the spine does not reach as far as the posterior tips of the postzygapophyses. It is slightly less produced in *P. muralis*, and slightly more acute in *L. vivipara.*

Sacral and cloacal vertebrae

There are nine vertebrae which have transverse processes rather than detached ribs, projecting perpendicularly from the centrum. Most of these vertebrae are relatively short in *L. vivipara* and *P. muralis,* and more elongate in *L. agilis*. The first two have robust cylindrical transverse processes, meeting distally though not fused. The first has its transverse processes slightly compressed in a vertical plane and the second has horizontally flared tips to its processes, which are indented where they connect to the anterior ends of the ilia. The first could therefore be known as the presacrum, and the second is therefore the sacrum. The next seven vertebrae can be described as cloacal (or postsacral) vertebrae. They are similar to the trunk vertebrae in form, but have wide, wing-like transverse processes rather than detached ribs, and become smaller and progressively more elongate posteriorly. Two of them are pathogenically fused in the *L. agilis* specimen. As with the trunk vertebrae, the more longer neural crest and greater size of *L. agilis* sacral and cloacal vertebrae aids separation from *L. vivipara* and *P. muralis*. The transverse processes of *P. muralis* are noticeably relatively longer and more slender than *L. vivipara*. In *L. viridis*, these vertebrae are correspondingly larger and more robust. The sacrum and presacrum have broad transverse processes with triangular cross-sections. These fit neatly together, as in the other species, but have strong cristata where the tips meet (see Figure 5.54c). The cloacal vertebrae have wide, flat transverse processes, tapering towards their tips, and the ventral keel is more deeply indented than in the trunk vertebrae (see Figure 5.54d).

Caudal vertebrae

In *L. agilis, L. vivipara* and *P. muralis*, each caudal vertebra is almost split into two halves by a fissure which runs transversely across the bone (see Figures 550b, 5.53b,d and 5.54e). Pratt (1946) described this as the autotomy plane. Attachment is only maintained by a short dorsal process, shared by the anterior and posterior halves. This is positioned mid-way along the dorsal surface of the vertebra, and has been described as the anterior neural spine (Pratt, 1946). The purpose of the fissure is clearly to facilitate autotomy of the tail. The area around the fissure is widened into flanges, which show signs of growth rings. The caudal vertebrae, in both species, also have an unfused haemal process. This is formed by a pair of haemapophyses, projecting from the ventrolateral sides of the centrum, and converging ventrally into a long process. When attached to the vertebra, it forms a haemal canal, but when detached it has the shape of a wishbone. In *L.*

viridis, the caudal vertebrae are relatively robust, and the fissure is much less obvious.

The caudal vertebrae of *L. viridis* are larger, more robust and shorter than the other species. There is a sharp, dorsally directed anterior neural spine above the fissure plane, and the posterior neural spine is long, as in the other vertebrae. *L. viridis* and *P. muralis* are also distinct from the other species as they possesses long, paired transverse processes, on either side of the fissure plane (see Figure 5.50b). The anterior pair are longer and wider, tapering towards their tips, the posterior pair are short and acute. *L. agilis* and *L. vivipara* lack these transverse processes, and probably have correspondingly weaker planes of fracture. In lateral view (Figure 5.53b,d), the caudal vertebrae of *L. agilis* are noticeably more elongate than those of *L. vivipara*. The position of a neural foramen may also be diagnostic. It is positioned mid-way up the neural walls in *L. agilis*, towards the posterior end of the anterior section, but is positioned much lower down in *L. vivipara*. The posterior neural spine (Pratt, 1946), cf. the neural spine of other vertebrae, is of typical form for all four species.

PECTORAL GIRDLE

Scapulocoracoid

This bone consists of a long, flat rod (scapula) and a broadly flared fan (coracoid), similar to that of the newts. The coracoid part has a narrow process radiating dorsally from the glenoid fossa, and a small round fenestra is enclosed towards its base. The glenoid cavity is not cup-shaped as in the newts, but semicylindrical as in mammals. The scapula part is slightly narrower and more elongate in *L. agilis*, and slightly more flared in *L. vivipara*. *P. muralis* has more slender processes than *L. vivipara*, and size differences may aid diagnosis, but reliable diagnostic criteria have not been isolated. The overall length of the scapulocoracoid is 3.5mm in *L. vivipara*, compared with 5.6mm in *L. agilis*.

PELVIC GIRDLE

The pelvis is trifurcate and each half is formed from an ilium, pubis and ischium. These are fused in adults, but a symphysis is still visible. In fossil specimens, these elements can remain fused, but their collective shape is unwieldy and tend not to survive entirely intact. The angle between the margo ventralis of the ilium and the margo anterior of the pubis forms a broad curve. This is wider (more obtuse) in *L. vivipara* than in *P. muralis*.

Ilia

The ilia are similar in form to the anuran ilium. They have a cup-shaped acetabulum at the proximal end, and an elongate blade extending anteriorly, and tapering to a narrow tube which connects with the transverse processes of the sacrum. There is a distinct tuber superior, above the anterior margin of the acetabulum. The ilium is relatively thin in *L. agilis*, but is relatively thicker and more robust in *L. vivipara*. The tuber superior is more pointed and directed slightly posteriorly in *L. agilis* and

strongly posteriorly in the *P. muralis* specimen. It is more bulbous and roughened in *L. vivipara* specimen. *L. viridis* could be separated by its larger size. As intraspecific variability has not been assessed, it is not certain that these features are reliably constant.

APPENDICULAR SKELETON

The smallest limb elements are minute and fragile. They are unlikely to survive in fossil assemblages or be retained in a 250 micron sieve.

Humeri

The humeri are of similar proportions and morphology, but again there is a distinct size difference, particularly for *L. viridis*. The *L. vivipara* specimen has its epiphyses fused; these appear to be robust and have retained the detailed morphology of the proximal articulation. Epiphyses in amphibians normally remain cartilaginous throughout life. It is not known whether this is the case in lizards, but the *L. agilis* specimen was an adult and lost its epiphyses during preparation. The *L. vivipara* specimen was probably a very mature animal. The total length of the humerus (without epiphyses) was measured at 7.8mm in *L. agilis*, and 5.1mm in *L. vivipara*. Sexual dimorphism is normal in lacertids, where females tend to have relatively shorter limbs (Arnold and Burton, 1978). This is likely to be reflected in limb bone lengths.

Femora

The proximal portion of the femur is noticeably more elongate in *L. agilis* than in *L. vivipara*. The femur is also more slender overall in *L. agilis*. It is more flared at its ends in *L. vivipara*, with the shaft constricted. A dorsal ridge along the proximal shaft is more acute in *L. agilis*. Total length (without epiphyses) is 8.5mm in *L. agilis*, and 5.8mm in *L. vivipara*. Again, *P. muralis* is intermediate in size and proportions.

5.12 Anguidae

(*Anguis fragilis*)

A. fragilis is perhaps the most osteologically distinct member of the modern British herpetofauna and has no close relatives with which to be confused. Its recently-recognised closest relative *Anguis cephallonicus* is endemic to southern Greece (Gasc *et al*, 1997). The only other Anguid in Europe is *Pseudopus apodus*, which has a wide Balkan distribution (Gasc *et al*, 1997). Its much greater size and distinct osteology allows easy separation. The family Anguidae contains North American members with four fully-functioning limbs, but the two European genera are entirely legless, and constitute a derived and regressive body form (Smith, 1969). The slow-worm's skeleton does not previously appear to have been systematically described. Estes (1983) highlights the lack of such descriptions as a persistent problem in lizard osteology. An overview of the skeleton of *A. fragilis* was provided by Gleed-Owen (1997f).

Smith (1969) suggested that both pectoral and pelvic girdles are present in vestigial form. There appears to be no evidence of appendages, nor of a pectoral girdle, judging by the specimens seen. A remnant pelvic girdle is present, and is described below. It may be the case that it has been reduced to such small bones that only occasional examples possess them. Alternatively, some evidence may have been lost during laboratory preparation. Evisceration would have to be extremely careful to be very careful to prevent loss of what might be very lightly attached bones. It is unlikely that the maceration techniques used could destroy these bones, as minute and intricately ornamented bones do normally survive unharmed. Smith (1969) gave brief notes on the skull, caudal vertebrae and osteoderms, with good illustrations of each. Estes (1983) detailed the existing European records of fossil anguids.

A. fragilis has a very distinct skeleton. Fossil occurrences of vertebrae and osteoderms are by far the most common, and isolated remains can often be distinguished immediately. Some of the thicker (hence more durable) cranial elements, such as the parietal and dentaries, may also be found. Five comparative specimens have been studied so far. Osteological nomenclature follows that of Rage (1984) and Szyndlar (1984) on snake vertebrae, and Estes (1983) on lizards.

CRANIAL BONES

A. fragilis has a highly-ossified cranium to suit its fossorial existence (Smith, 1969). It is of a typically Saurian nature, and Smith (1969) illustrated it in detail. For palaeontological purposes, some of the elements may actually be identified from these drawings, as the skeleton of *A. fragilis* is so distinct. However, there is room for confusion with bones of lacertid lizards. The parietal (Figure 5.55a) and frontals form the dermal roofing of the cranium. Their surfaces are also furnished with a rugose relief, formed by the fusing of osteoderms to them. The reticulate pattern of the osteoderms covers the dorsal surface of the parietal and frontals. These elements also exhibit rugose surface patternation (exostosis) of a very similar nature, in the examples of *L. agilis* and *L.*

vivipara studied. Further work is required in this area to enable identification of fossil cranial elements. An SEM photographic key might be useful, but as these elements appear infrequently as fossils, this has not been made during the current study.

VERTEBRAE

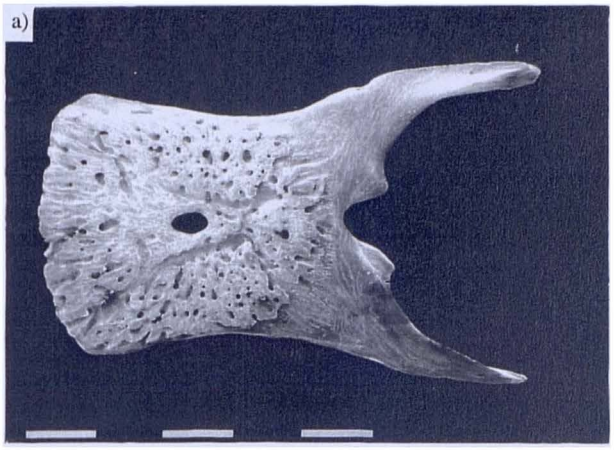
The vertebral column can be divided, into cervical (about 6 vertebrae), trunk (about 45 vertebrae), cloacal/sacral (2 or 3 vertebrae), and caudal (about 55 vertebrae) regions. In general morphology, the caudal vertebrae form a distinct group, as do all the other vertebrae.

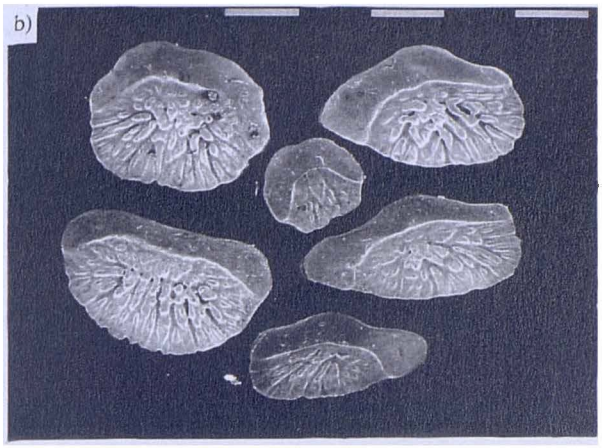
Cervical vertebrae

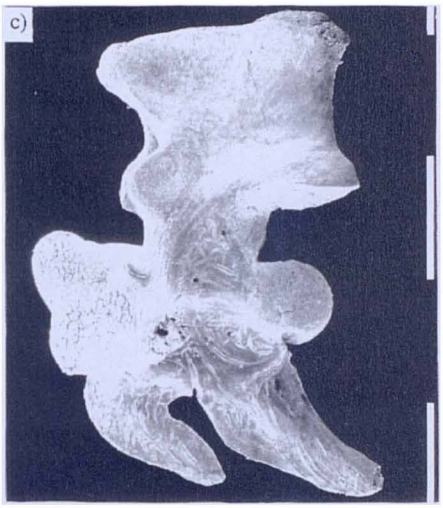
There are around six vertebrae which can be described as cervical. The first two are fused together at the centrum, and have very clearly defined ventral processes (see Figure 5.55c). This bone essentially consists of the atlas centrum fused with that of the axis vertebra. The rest of the atlas consists of three separate parts, a character also found in the Lacertidae and Ophidia. The anterior cotylar articulation (for meeting the occipital condyle) is made up of facets from all three parts (see Figure 5.55d). There is a symmetrical centrum with a posteroventrally-directed hypapophysis, tapering to a point as in most snakes. The centrum is short and rounded anteriorly, apparently to facilitate the lateral portions of the compound atlas. These bones are formed of a small bifaceted disc, extending dorsally as a curved leaf-like plate: essentially the two halves of the neural arch. The lower faceted parts fit, like wedges, between the opposing articular facets of the occipital condyle and the cotyle of the atlas. The dorsal extensions curve around either side of the neural canal, and carry rudimentary postzygapophyses midway up, which articulate with opposing features on the second vertebra. The proceeding cervical vertebrae are more like trunk vertebrae in form, each with a strong neural arch, spine, zygapophyses and a progressively longer centrum and smaller ventral process.

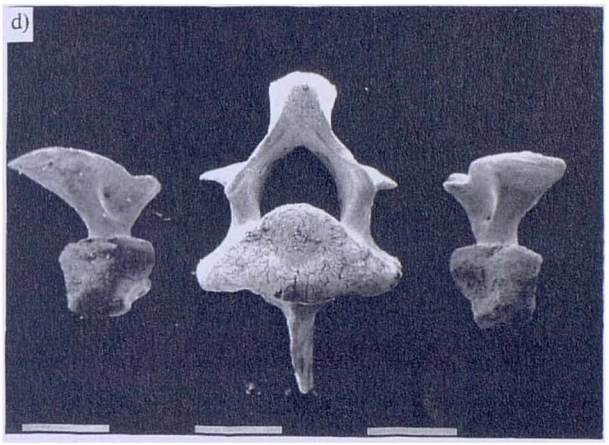
Trunk vertebrae

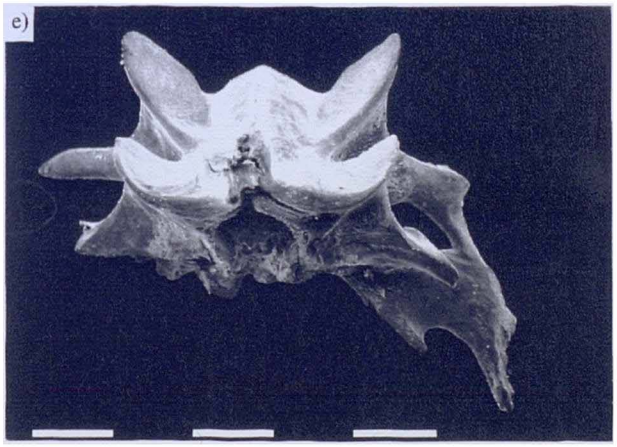
See Figures 5.51-5.53. The first of the trunk vertebrae are shorter, and transitional in form between the last cervical vertebrae and middle trunk vertebrae, differing also by their lack of a ventral process. Otherwise, their shape and proportion is fairly consistent throughout the trunk region. The centrum is stout and is shouldered ventrally, giving it a flat underside. The foramen nutritius passes through it towards its anterior end. It is broadened anteriorly to accommodate the lateral paradiapophyses. The neural arch and neural spine are robust, the latter is thicker towards its posterior end. It extends as a uniform wall, anteriorly almost to the prezygapophyses, and midway along the postygapophyses (similar to that of the newts). The zygapophyses are angled at around 40°, with only their margins unsupported. The strong posterior articulations and posterior neural arch give the impression of strengthening in a vertical plane, in the same way that the anterior end of the vertebra is strengthened horizontally by its robust paradiapophyses.











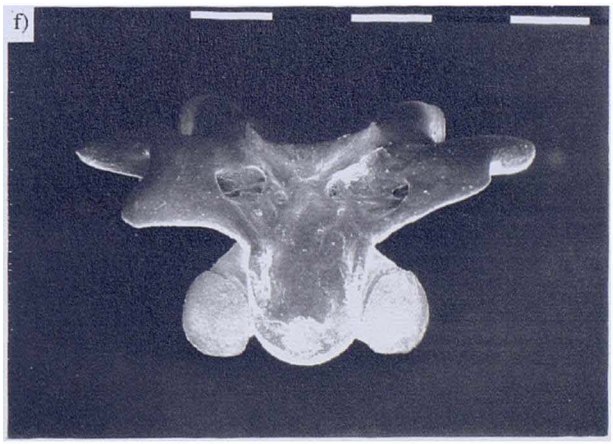


Figure 5 *55A. fragilis*: a) parietal (CGO 16/5), dorsal view; b) osteoderms (CGO 16/), external view; c) axis (second) vertebra (CGO 16/4), left lateral view; d) atlas and axis vertebrae (CGO 16/4), anterior view with atlas sections rotated 90º laterally; e) pathological sacrum (CGO 16/4), anterodorsal view; f) cloacal vertebra (CGO 16/4), ventral view.

Sacral vertebrae

The two cloacal or sacral vertebrae are of the same basic form as the trunk vertebrae, but are provided with wide and broad pleurapophyses. In one specimen seen (CGO 16/4), these are ventrolaterally directed and appear to consist of two pairs of transverse processes. These are united along their lengths, and project from the posterior sides of the centrum. The longer of each pair, is bent downwards further, and forms the narrower distal portion of the process. These are analogous to the forked lymphapophyses seen in snakes (Rage, 1984; Szyndlar, 1984). This vertebra also possesses a pair of short basal ridges (haemal keels), beneath the posterior ventral edges of the centrum, connected to the proximal ends of the transverse processes. The other sacral vertebra of the same specimen is apparently a congenital fusion of one and a half vertebrae. Its assymmetrical outline has much larger, wider and broader transverse processes, possibly resulting from the fusion of an additional pair of transverse processes. The resulting lateral projections on the left hand side, are smaller and more simple than the large fenestrate wing-like projection on the right hand side, which has originated from perhaps four separate processes. It is likely that the anterior tips of the ilia articulate with the ends of these transverse processes. Thus this is probably the sacrum proper.

Caudal vertebrae

The caudal vertebrae have been briefly described by Smith (1969), with relation to their function in autotomy. Pratt (1946) gave an account of the plane of fracture in *A. fragilis*, and illustrated a caudal vertebra. Figures 5.53f and 5.56a-d shows details of *A. fragilis* caudal vertebrae and the plane of fracture. The overall form of the caudal vertebrae is more elongate than in the trunk vertebrae. The centrum is more slender, the zygapophyses are closely positioned and steeply tilted. The bone is much less robust in its appearance, mainly due to the lack of bulky paradiapophyses, which are instead replaced with (pointed laterally-directed) pleurapophyses, which are effectively fused ribs (Rage, 1984). The neural spine is unlike that of the trunk vertebrae, but is instead produced as a posteriorly-directed crest, extending as far as the tips of the postzygapophyses. In lateral view, it is similar in shape and proportion to the neural spine of *L. agilis* trunk vertebrae. There is a long ventral projection, curving posteriorly, consisting of a haemal arch and finishing as a narrow point. A pair of wide transverse processes extend from the centrum, with a very slight downwards tilt, and angled slightly anteriorly.

The most distinct feature of the caudal vertebrae is the mechanism which facilitates autotomy. Towards the anterior end of each vertebra, a suture passes right across the neural arch and centrum, and into the transverse processes. It becomes indistinguishable towards the tips of the processes, which hold the two halves of the vertebra together. In effect, each caudal vertebra is made of two halves, each of which share only the tips of the transverse processes. The suture is apparently present at all times during the growth of the animal, and when a caudal vertebra is split into halves, concentric growth rings can be seen radiating outwards from the neural canal. Clearly

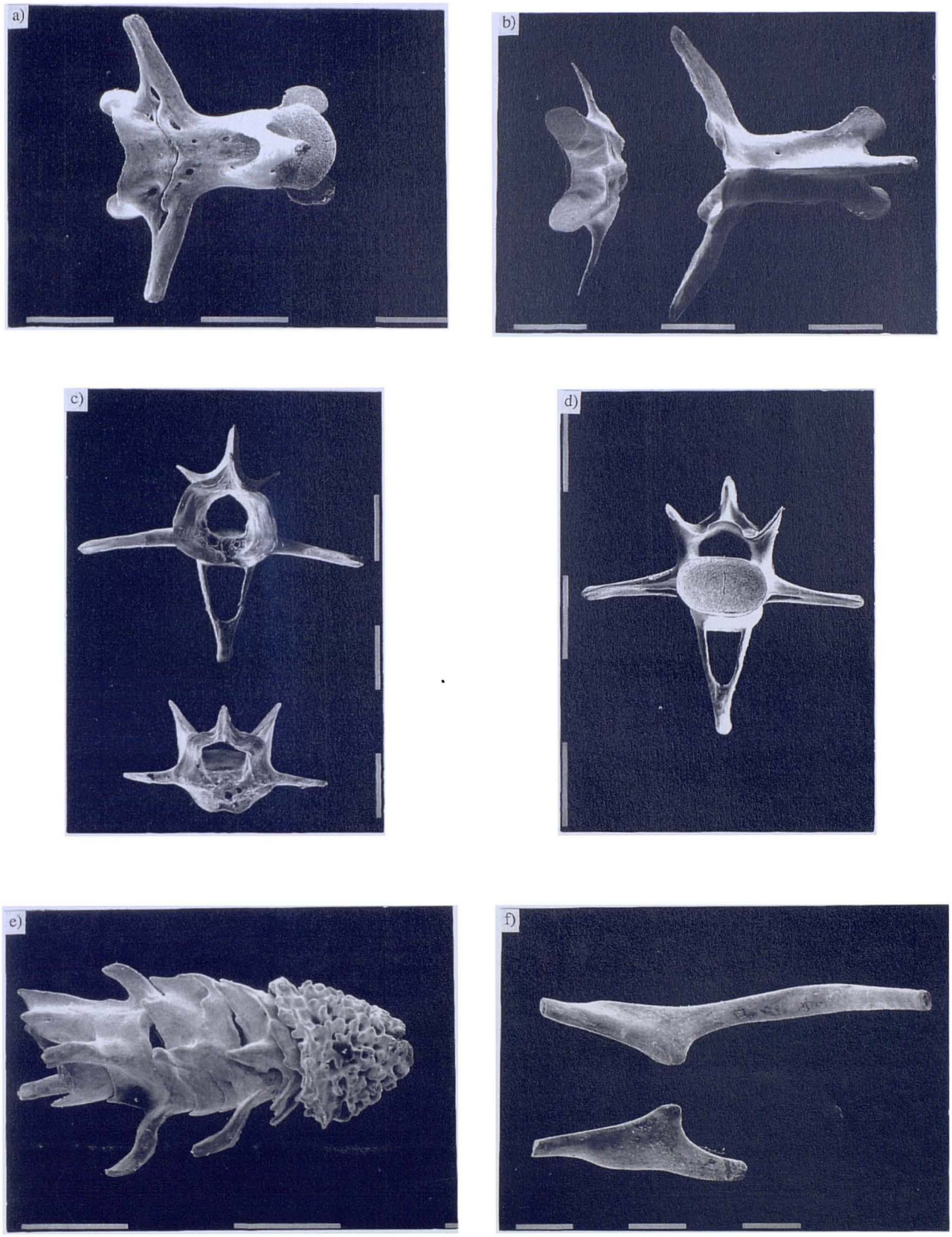


Figure 5.56: *A. fragilis*: a) caudal vertebra (CGO 16/1), ventral view; b) caudal vertebra separated along suture (CGO 16/5), dorsal view; c) caudal vertebra separated along suture (CGO 16/5), anterior view of posterior half (top) and posterior view of anterior half; d) caudal vertebra (CGO 16/5), anterior view; e) fused distal caudal vertebrae (CGO 16/5), left lateral view; f) pelvic girdle (CGO 16/4).

no movement is possible along this fracture line, and rigidity of the bone relies on the leaf-spring nature of the transverse processes. Throughout life, as the animal grows, enlargement of this flange takes place on both halves, by addition of larger rings of bone. Whilst the opposing faces remain unattached, their surfaces are close-fitting. The expanded flanges are prominent when an intact vertebra is viewed laterally. Their presence may be related to the attachment of the muscles which are contracted in order to break the vertebra during autotomy.

Distal caudal vertebra

The distal caudal vertebra is also of note, consisting of at least four fused vertebrae, bearing dorsal, ventral and transverse processes. The posterior section is formed probably from one or more amalgamated vertebrae, but their form is unrecogniseable, being rounded into a bulbous boss, with a rugose honeycombed texture (Figure 5.56e). This amalgamation of end-tail vertebrae is typical of snakes, particularly the erycines (Szyndlar, 1994). This bone is an probably unlikely to be found as a fossil occurrence, due to there being only one of its kind in *A. fragilis*' skeleton. There would be approximately a hundred other vertebrae for each distal caudal vertebra, but it should be robust enough to survive otherwise. There may be other value in finding single bones such as this, for assessing numbers, sizes and ages of individuals, but as yet none have been found fossil.

PECTORAL GIRDLE

Smith (1969) claimed that *A. fragilis* possesses a remnant pectoral girdle, but no evidence of this has been found.

PELVIC GIRDLE

The presence of a vestigial pelvic girdle has been noted previously (Smith, 1969), but does not appear to have been described. In the specimens studied here, pelvic elements have been observed in all specimens. The girdle is in the form of a pair of elongate curved rods, widened at one end (Figure 5.56f). This is probably the posterior end, forming the remnant of the main ilial corpus. Romer (1956) illustrated the remnant pelvis in *P. apodus*, showing that it has an acetabulum and consists of an elongate ilium, a flattened pubis and a minute ischium. The remnants in *A. fragilis* seen so far, are more reduced and fused into one unit. The rudimentary femur which is present in *P. apodus* (Romer, 1956) has not been found in *A. fragilis.* However, the anteroventral corner of each element may be the remnant of a fused femur, and the elongate, tapered anterodorsal rod is likely to be the ilium. The anterior tips of these ilia are tubular and probably connect with the transverse processes of the sacrum. It is not known whether they are anatomically important in protection of the cloacal region. The individual ilium must be less likely to be encountered fossil than other more robust and more numerous bones of the skeleton.

OSTEODERMS

The most distinctive feature of the skeleton, which sets *A. fragilis* apart from all other northwest European reptiles, is the presence throughout the skin of a chainmail-like covering of bony scales, known as osteoderms. These are independent centres of dermal ossification. The parietal and frontals of the cranium are overlain with osteoderms, which it appears are fused to them, rather than growing as exostotic bone. The resulting rugose patterning on the dorsal surfaces of these bones is particularly well developed in mature individuals. There are twenty-six rows, encompassing the body, along its whole length, forming an imbricated shield. Smith (1969) reports that the number of rows is consistent, at least among British specimens. As each osteoderm overlaps the next one, rings of osteoderms are spaced around 1-2mm apart. It is estimated that there are in excess of 6-7,000 in each individual animal. One specimen, which had lost most of its tail, possessed 3,310 osteoderms (C. Price, pers. comm.). The osteoderms are positioned in rows along the body and tail, staggered so that each individual osteoderm is surrounded by six others, in a hexagonal pattern. Thus only around half of each osteoderm is visible, affording maximum protection, whilst still permitting maneouverability. Each osteoderm is formed of a disc of bone, curved to fit the body, and varying in shape according to the body position. Outline shapes range from sub-hexagonal to elongate, with various polygonal and sub-hemispherical shapes (Figure 5.55b). Only those along the dorsal and ventral median rows are symmetrical. Each osteoderm is thickest around its anterior edge, where it is attached, and wedges out around towards its free edges, which are more irregular in outline. The lower surface is smooth, and punctuated usually by two transversely-aligned central foramina. Growth rings are visible around the thinner and translucent posterior free edges. Most of the upper surface is rugose and consists of a radiating network of channels and intervening ridges. Smith (1969) described the system of grooves as circulatory channels. The anterior edge of an osteoderm may be seen as the proximal portion, relatively straight and angular in outline. It is the thickest part and is smooth on both surfaces. The smooth area on the upper surface is parallel to the outline of the anterior margin, and may be seen as delineating the proximal portion. This part can cover from around a fifth to a half of the surface area of each osteoderm, forming much of its outline. The rest may be seen as the distal portion, and is relatively free of attachment. It diminishes in thickness towards its margins, and is deeply sculpted with a network of channels, separating a maze of upstanding ridges. The pattern radiates from near the centre of the osteoderm (the anterior part of the distal portion), towards the posterior and lateral edges. Osteoderms are so distinctive that it does not take specialist knowledge to identify them. Nonetheless, it is probable that many workers have found unidentifiable but highly distinctive scale-like objects belonging to this category.

5.13 Ophidia (Colubridae, Viperidae)

(Coluber viridiflavus, Elaphe longissima, Natrix natrix, Natrix maura, Natrix tessellata, Coronella austriaca,Vipera berus, Vipera aspis)

Boulenger (1914) published early texts on the snakes of Europe, but with only limited osteological description. The situation has now been remedied to a large degree. Rabeder (1977) discussed the comparative osteology of cranial bones, providing some diagnostic descriptions. He illustrated many ophidian cranial elements, including those of *E. longissima, N. natrix* and *V. berus*. Markert (1974) provided a key for the distinction of German fossil snakes, using detailed characteristics of trunk vertebrae. Szyndlar (1984) fairly comprehensively described and figured snake vertebrae and cranial elements of Polish fossil snakes, with attempts at identification keys. He has subsequently published many fossil snake faunas, most notable for their informative descriptions and excellent illustrations. His discussions of a comparative nature are very useful, raising important points for consideration (e.g. Szyndlar, 1984; 1991). He has also studied intracolumnar variation and intraspecific variation quite extensively, suggesting that caution should be taken when diagnosing trunk vertebrae (Z. Szyndlar pers. comm., 1995). This would appear to be in conflict with earlier works, such as Markert's (1974) key.

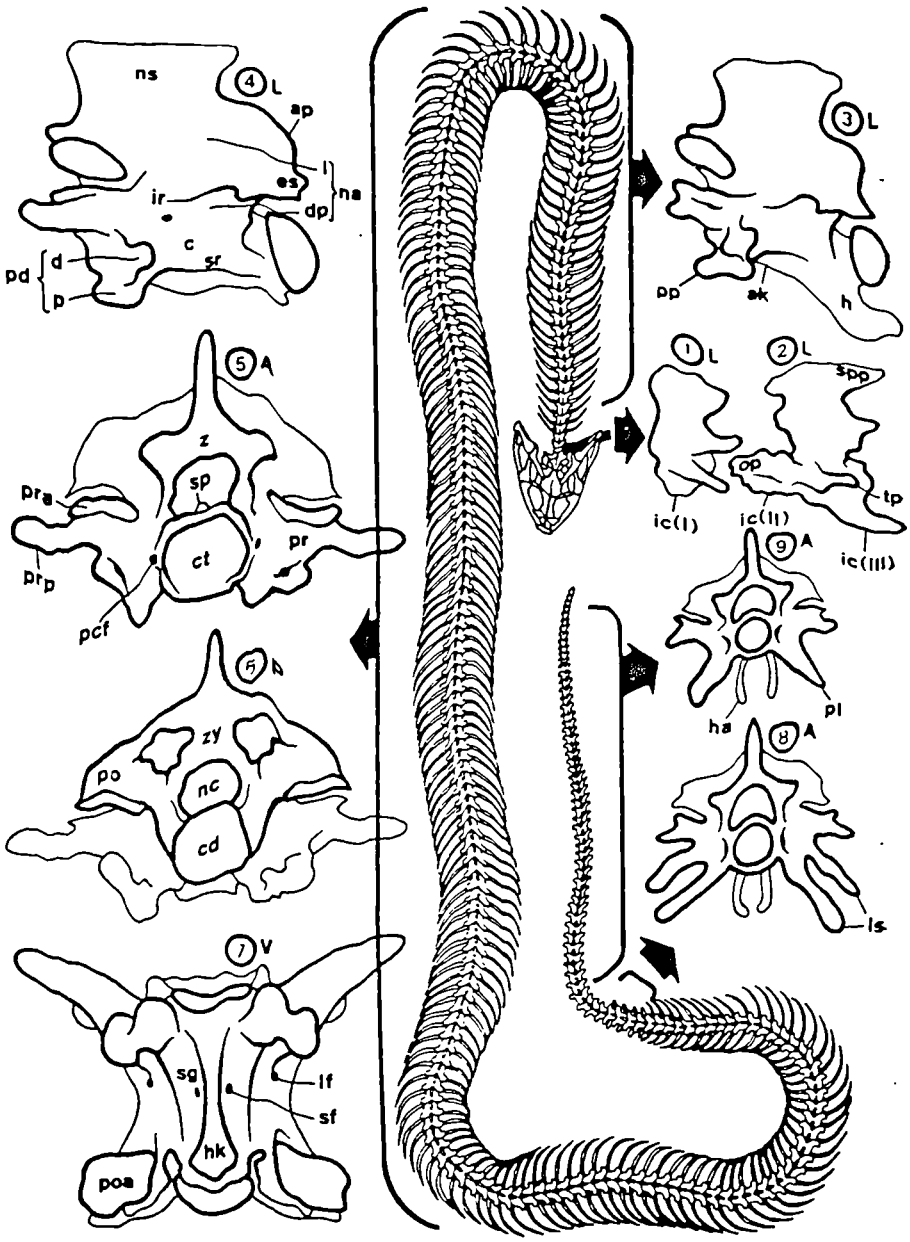
Hecht (1988) raised important issues concerning intracolumnar variation of snake vertebrae and the problems it potentially poses to palaeoherpetology. J.C. Rage has also carried out extensive work on French ophidian fossil material, and reviewed the European fossil snake record (Rage, 1984). Considering the large volume of continental literature on fossil ophidians which has been published to date, a satisfactory identification key is still conspicuously lacking.

Three *N. natrix*, one *N. maura*, one *C. austriaca* and one *V. berus* have been collected during the current study. These are detailed in Appendix 1. Skeletons of *C. viridiflavus* (Ref. nos. MNCN 16320, 16321), *E. longissima* (MNCN 16327and *V. aspis* (MNCN 16427, 16428) were studied at the MNCN in December 1997. Unfortunately, no *N. tessellata* has been studied. From the literature (e.g. Holman *et al*, 1990) it appears that separation of *N. maura* and *N. tessellata* is difficult if at all possible. It is therefore assumed that *N. tessellata* can be recognised by the same features as *N. maura*.

It is clear from the existing literature, and from the British sites studied in this project, that almost all ophidian fossil material consists of isolated vertebrae. This is not surprising as these elements constitute most of the ophidian skeleton. This is reflected in the descriptive literature such as Szyndlar (1984, 1991), which deals mainly with vertebrae. For this reason, diagnostic criteria are discussed below for vertebrae only. Osteological nomenclature follows that of Rage (1974) and Szyndlar (1984).

CRANIAL BONES

Holman (1985) described a *C. austriaca* dentary from Ightham, Kent, but otherwise cranial



1 — atlas, 2 — axis (epistropheus), 3 — cervical vertebra, 4—7 — trunk vertebra (thoracic, dorsal, lumbar, precaudal, presacral vertebra), 8 — cloacal vertebra (sacral, pygal vertebra), 9 — caudal vertebra. Abbreviations: ak — anterior keel, ap — „aliform process" (pterapophysis), c — centrum (pleurocentrum), cd — condyle (vertebral condyle, ball of centrum), ct — cotyle (glenoid cavity, cup of centrum), d — diapophysis, dp — descending part of neural arch, es — epizygapophyseal spine, h — hypapophysis, ha — haemapophysis, hk — haemal keel (carina haemalis), ic (I) — intercentrum I (hypocentrum I), ic (II) — intercentrum II (hypocentrum II), ic (III) — intercentrum III (hypapophysis I), ir — interzygapophyseal ridge (zygapophyseal ridge, lateral ridge, margo lateralis, l — laminae (tectum), lf — lateral foramen (pedicular foramen, nutritive foramen, intervertebral superior foramen), ls — lymphapophysis, na — neural arch (neurocentrum), nc — neural canal (vertebral canal), ns — neural apine (neurapophysis, spinal apophysis), op — odontoid process, p — parapophysis, pcf — paracotylar foramen, pd — paradiapophysis = parapophysis + diapophysis (synapophysis, transverse process), pl — pleurapophysis, po — postzygapophysis (posterior articular process, posterior zygapophysis), poa — postzygapophyseal articular surface, pp — parapophyseal process (transverse inferior apophysis), pr — prezygapophysis (anterior articular process, anterior zygapophysis), pra — prezygapophyseal articular surface, prp — prezygapophyseal process (accessory process), sf — subcentral foramen (intervertebral inferior foramen), sg — subcentral groove (ventral fossa), sp — subneural process (epapophysis), spp — spinal process, sr — subcentral ridge (margo ventralis, margo inferior), tp — transverse process of atlas (pleurapophysis or pleurophysis), z — zygosphene, zy — zygantrum; A — anterior, L — lateral, P — posterior, V — ventral views. Not to scale

Figure 5.57: Typical colubrid snake skeleton (*Malpolon monspessulanus*), showing vertebral characters and nomenclature (after Szyndlar, 1984).

have been found very infrequently at British sites. Their osteology will not be described here. Szyndlar (1984) has discussed this subject systematically for Polish fossil ophidian material, and the illustrations provided by Rabeder (1977) for *E. longissima, N. natrix* and *V. berus* are also very useful.

VERTEBRAE

The vertebral column makes up the greatest part of the ophidian skeleton (see Figure 5.57). Based upon the form of vertebrae and of accessory features, cervical, trunk, cloacal/sacral and caudal regions can be isolated. Generally, vertebrae offer enough diagnostic information to allow specific determination from them. However, Hecht (1988) and Z. Szyndlar (pers. comm.) have called for care in the identification of snake vertebrae. Gradational variation in shape of the neural arch along the column is intrinsic, but this is also related to ontogenetic development. According to Hecht (1988), the problem is less significant in Pliocene and Pleistocene fossils than for earlier Tertiary fossils, as similarity with modern specimens can be assumed. Nevertheless, it is important to recognise which region of the column a vertebra comes from, to aid firm identification.

Snake vertebrae are procoelus, with a round, cup-shaped anterior articulation and a convex posterior articulation. There are additional pairs of small articular facets between the prezygapophyses, known as the zygosphenes, and between the postzygapophyses, known as the zygantra. These give the vertebral column greater strength and help prevent dislocation. Though vertical movement is limited, considerable lateral flexion is still possible (Saunders *et al*, 1969).

Figures 5.58-5.65 illustrate the vertebrae of the species studied.

Cervical vertebrae

Cervical vertebrae are recognised by their shorter centrum length, thinner sides (laminae), and their larger neural canal. In *Vipera* they are especially short and only two or three can be easily distinguished from the subsequent trunk vertebrae. The posterior neural arch is also typically more rounded and more highly vaulted than in the posterior trunk vertebrae. Cervical vertebrae of all species have a ventral spine known as a hypapophysis. This is posteroventrally directed and positioned close to the posterior condyle of the centrum. The hypapophysis is long and gracile in *Vipera* and *E. longissima*, whereas in *Natrix* it is shorter and more robust. In *C. austriaca*, the shape is intermediate between these genera. In *V. berus*, the tip is tapered and acute, whereas in *V.aspis*, it is broad along its whole length and has a an obliquely shouldered tip. In *N. maura* the tip is more acute than in *N. natrix*, where it is rounded. Though no *N. tessellata* has been seen, its osteology is apparently very similar to that of *N. maura* (Holman *et al*, 1990)).

For diagnosis of cervical vertebrae, the posterior neural arch (seen in posterior view) should be considered, in addition to the shape of the hypapophysis which is not sufficient alone. In *Natrix*, the neural arch is high, with a semicircular profile. In *E. longissima* it is steeply vaulted, and viewed posteriorly there is a characteristically indented area at the base of the neural spine.

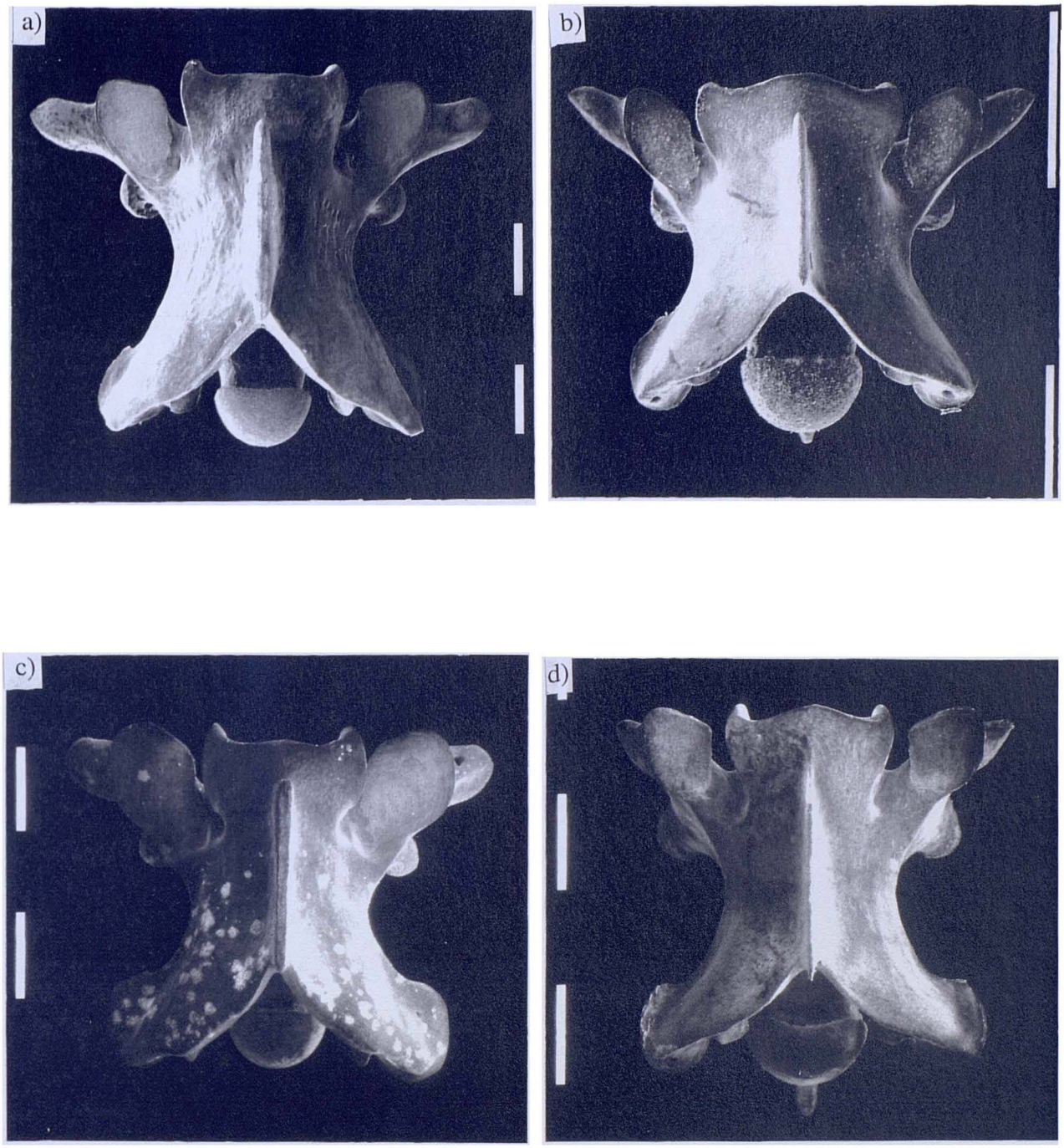


Figure 5.58: Trunk vertebra (dorsal view) of: a) *N. natrix* (CGO 13/1); b) *N. maura* (CGO 3/1); c) *C. austriaca* (CGO 28/1); d) *V. berus* (CGO 20/1).

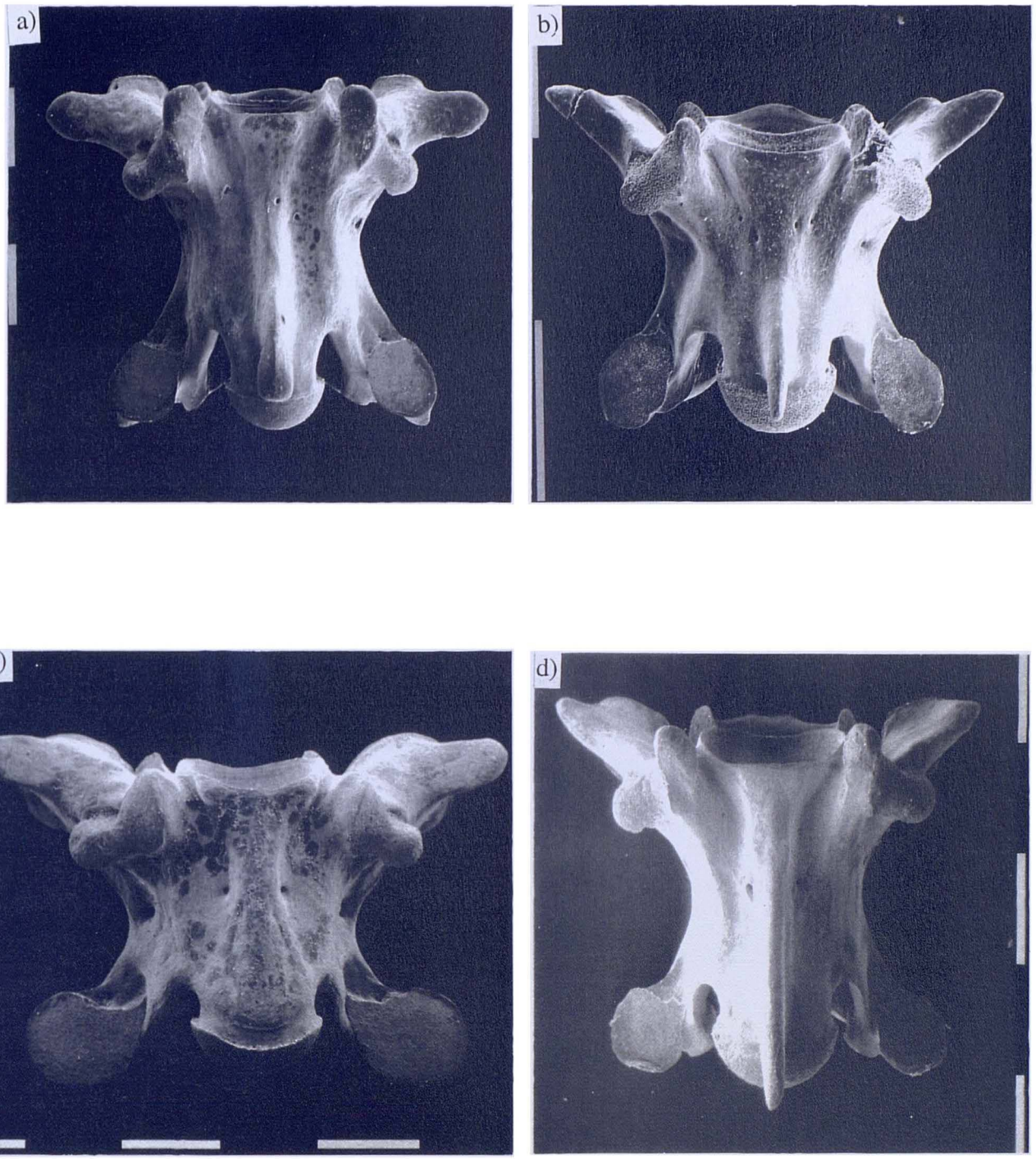


Figure 5.59: Trunk vertebra (ventral view) of: a) *N. natrix* (CGO 13/1); b) *N. maura* (CGO 3/1); c) *C. austriaca* (CGO 28/1); d) *V. berus* (CGO 20/1).

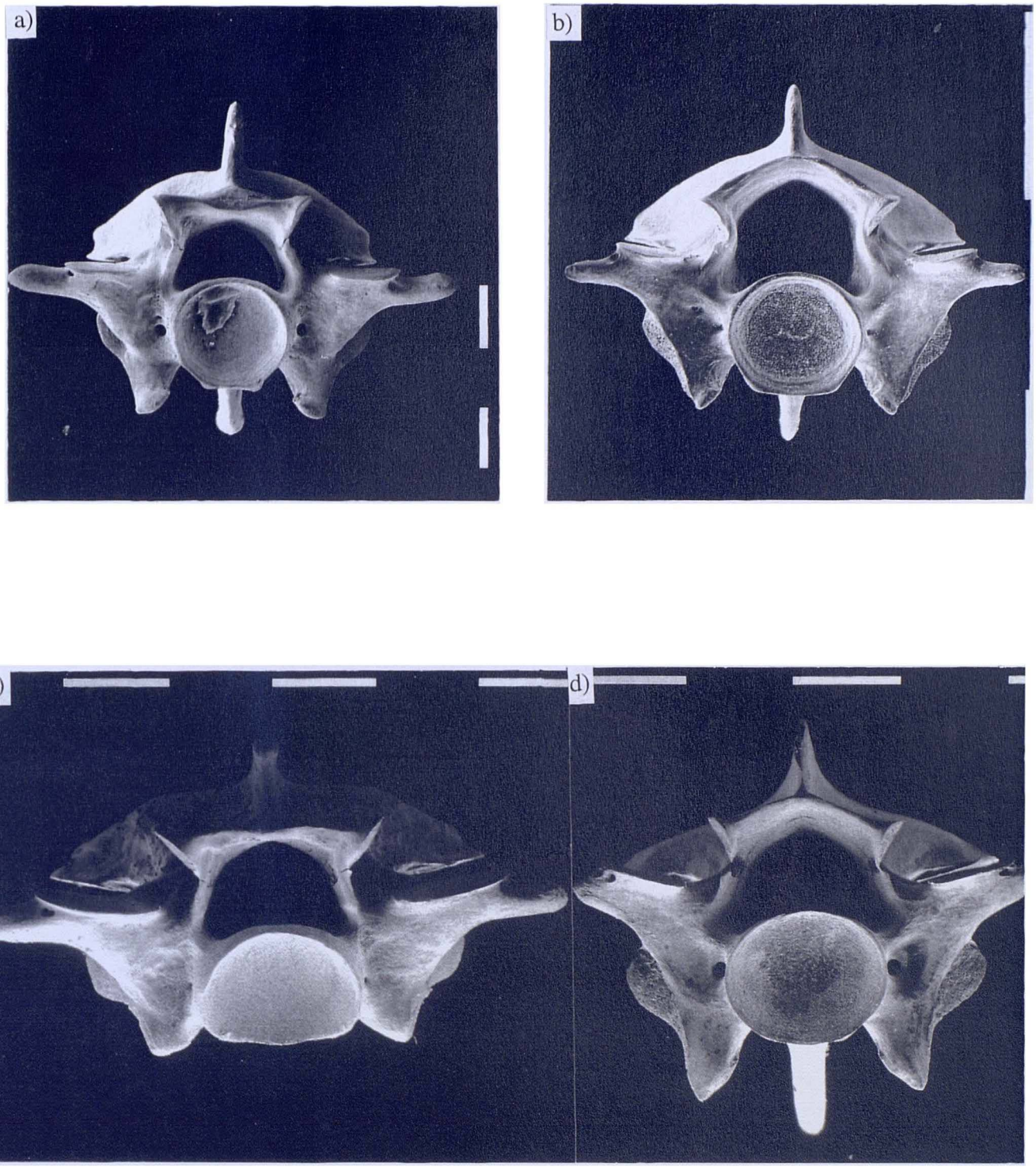


Figure 5.60: Trunk vertebra (anterior view) of: a) *N. natrix* (CGO 13/1); b) *N. maura* (CGO 3/1); c) *C. austriaca* (CGO 28/1); d) *V. berus* (CGO 20/1).

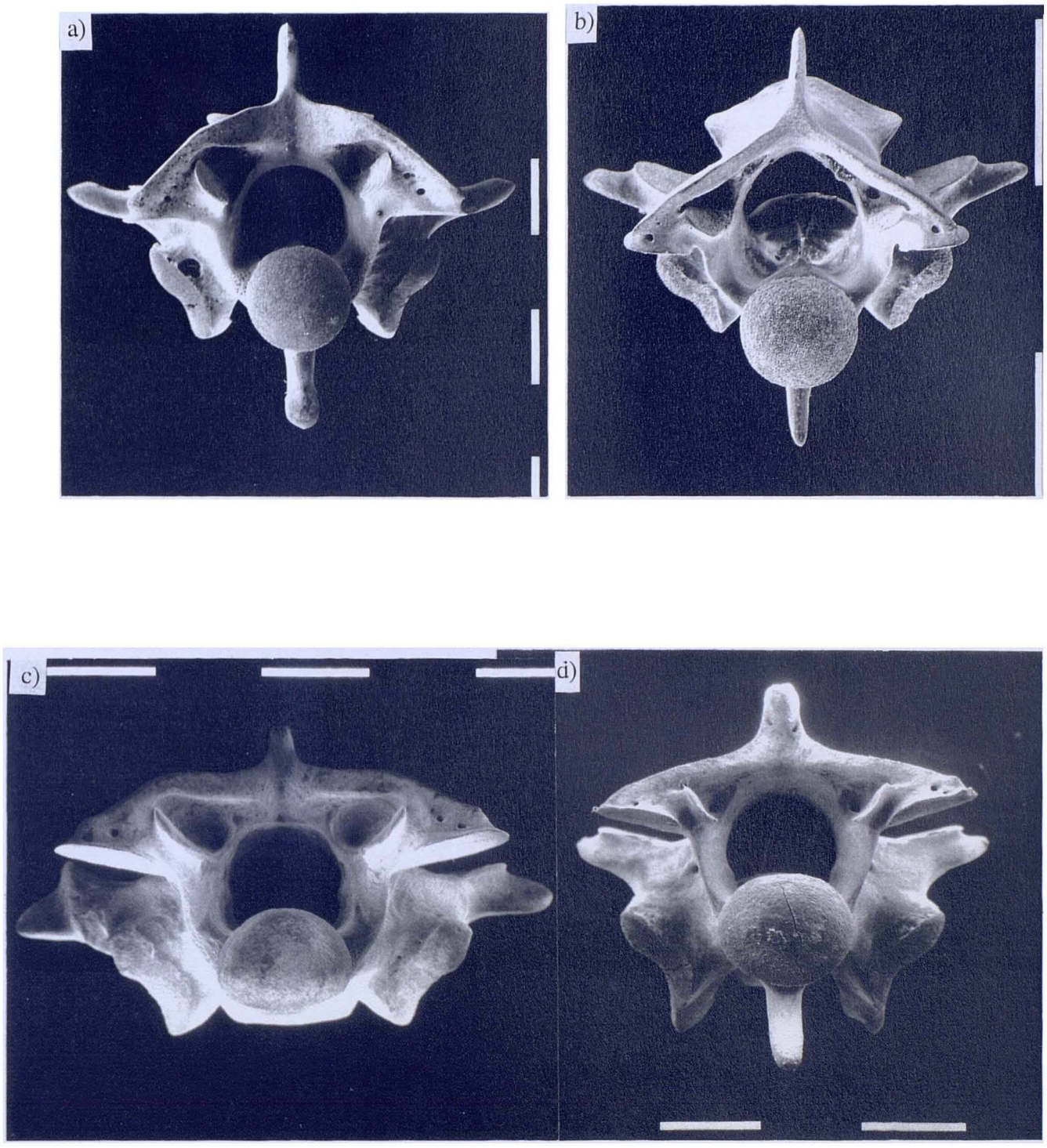


Figure 5.61: Trunk vertebra (posterior view) of: a) *N. natrix* (CGO 13/1); b) *N. maura* (CGO 3/1); c) *C. austriaca* (CGO 28/1); d) *V. berus* (CGO 20/1).

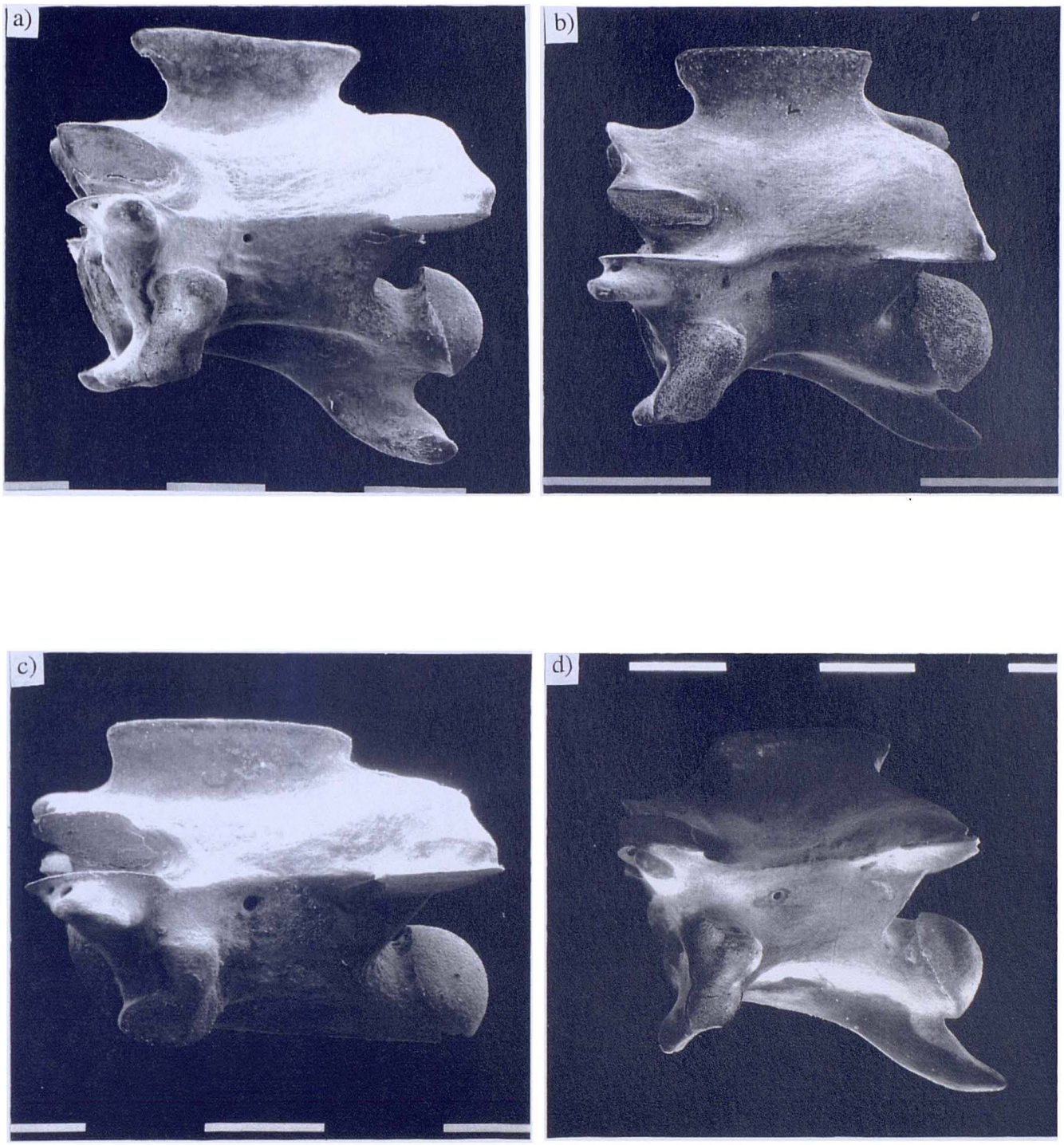


Figure 52: Trunk vertebra (left lateral view) of: a) *N. natrix* (CGO 13/1); b) *N. maura* (CGO 3/1); c) *C. austriaca* (CGO 28/1); d) *V. berus* (CGO 20/1).

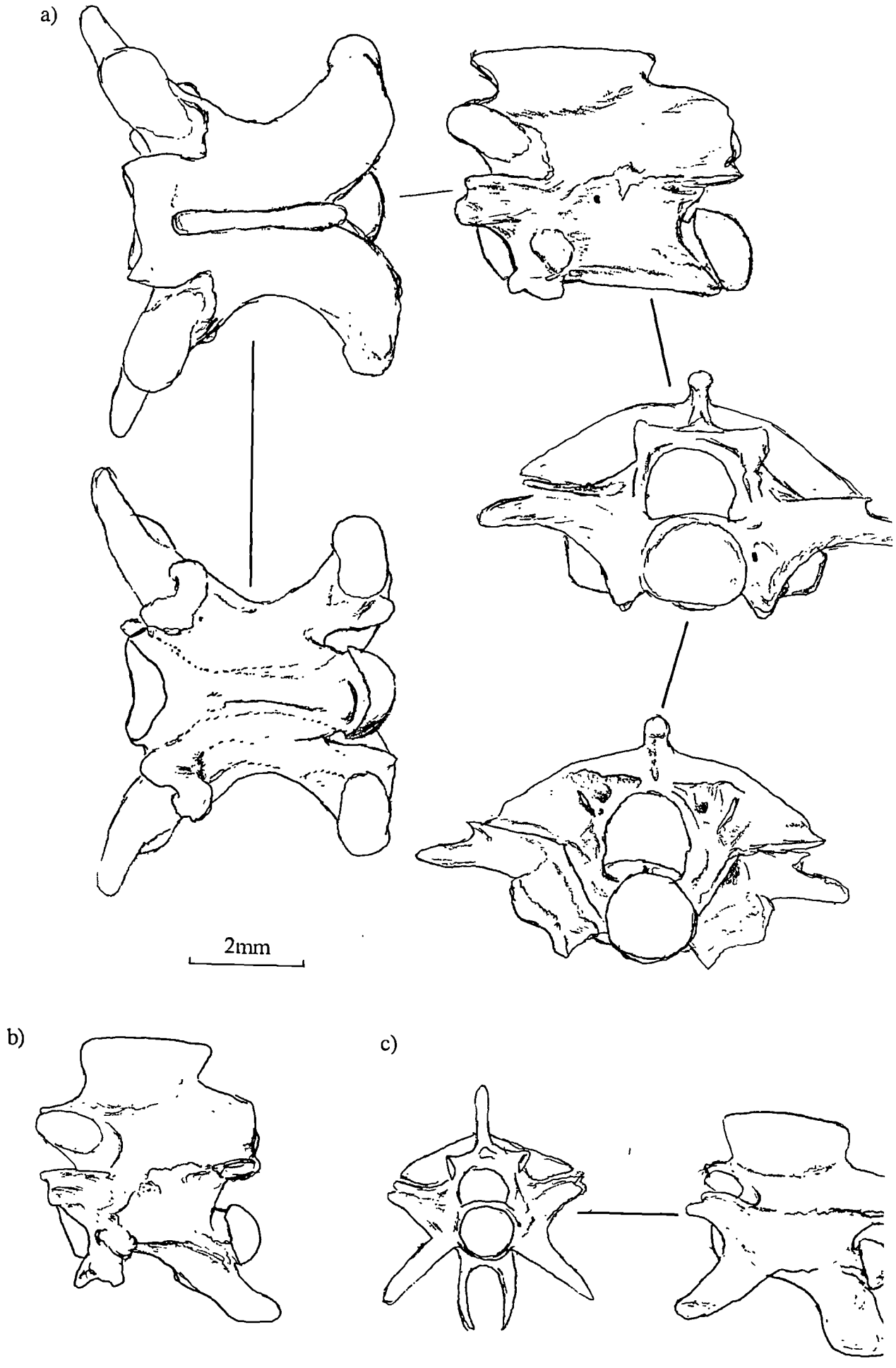


Figure 5.63: *C. viridiflavus* (MNCN 16320, Spanish specimen): a) mid-trunk vertebra; b) cervical vertebra, left lateral view; c) caudal vertebra, anterior and left lateral views.

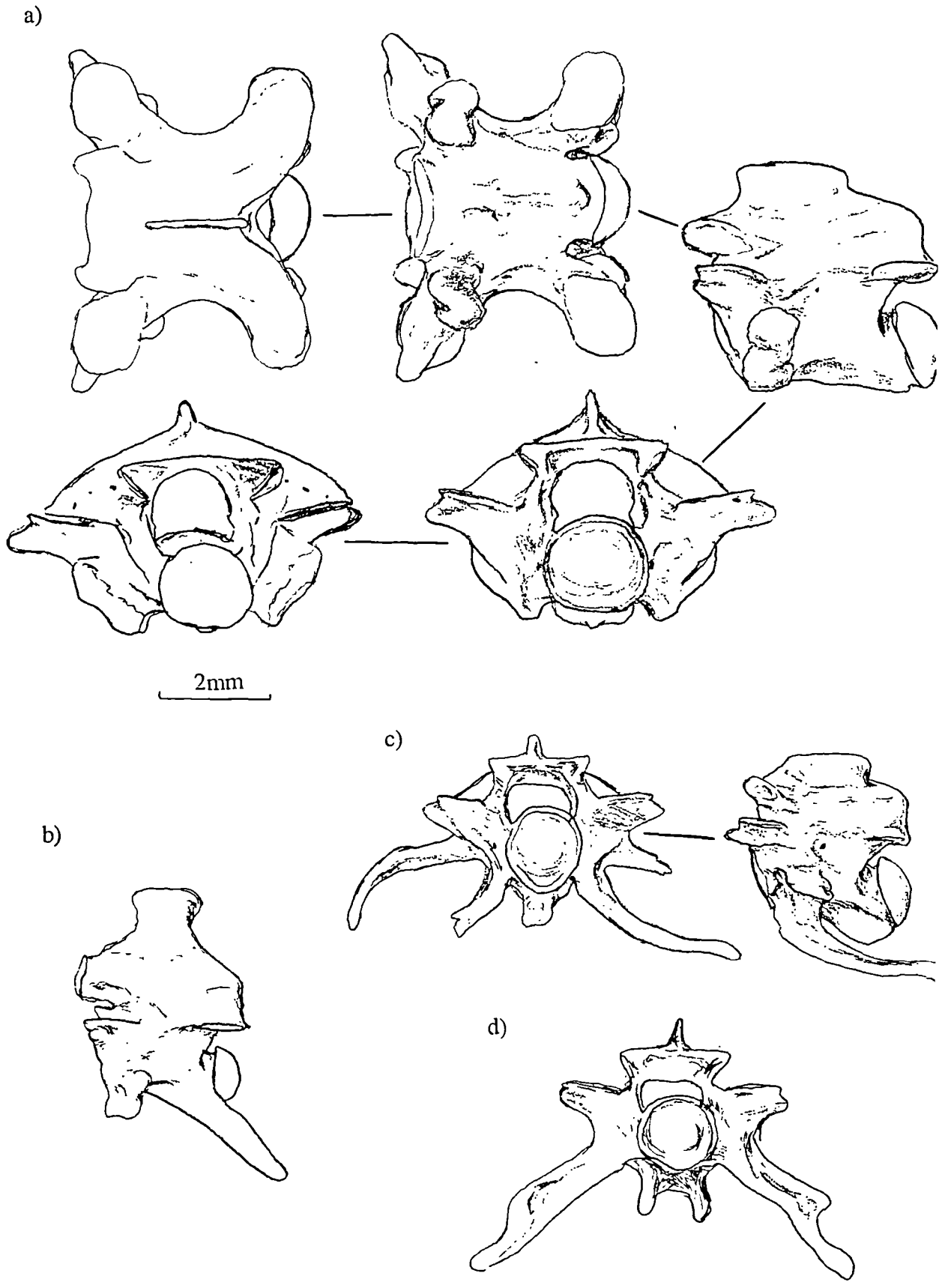


Figure 5.64: *E. longissima* (MNCN 16327, Spanish specimen): a) mid-trunk vertebra; b) cervical vertebra, left lateral view; c) anterior caudal vertebra, anterior and left lateral views; d) caudal vertebra (third beyond bone shown in 'c'), anterior view.

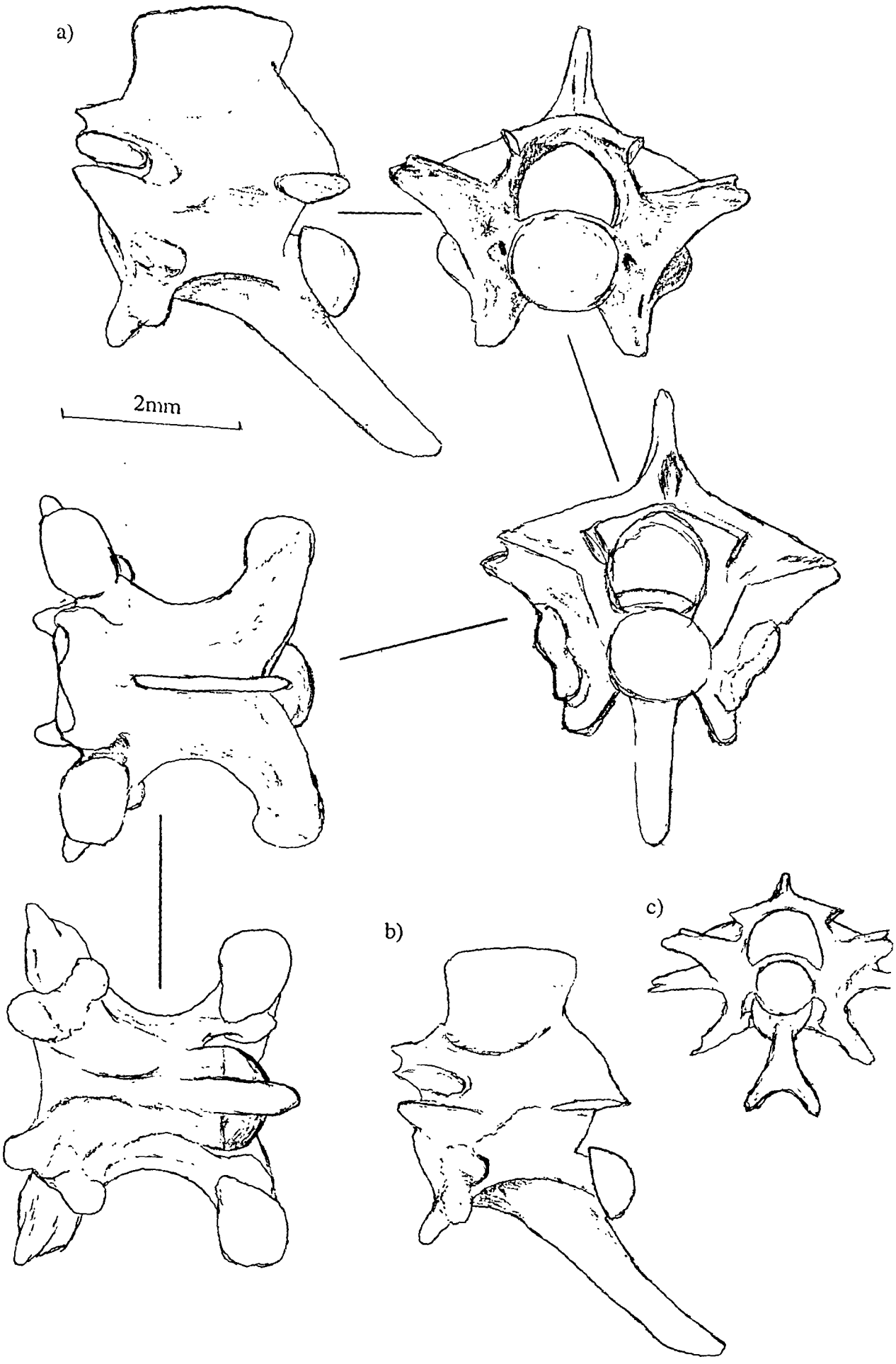


Figure 5.65: *V. aspis* (MNCN 16427, Spanish specimen): a) mid-trunk vertebra; b) cervical vertebra, left lateral view; c) caudal vertebra, anterior view.

Viewed dorsally, the rim of the posterior neural arch is visible due to its bevelled edge. In *C. austriaca* and *C. viridiflavus*, cervical vertebrae are vertically compressed, with the posterior neural arch low, flat-topped and distinctly shouldered. In *Vipera*, the neural arch forms a low arc.

Trunk vertebrae

Trunk vertebrae are the most commonly found skeletal elements of fossil snakes. They are also diagnostic in most cases with a good degree of certainty, though Z. Szyndlar (pers. comm.) has some reservations when intraspecific variation is considered fully.

The hypapophysis is long in both *Natrix* and *Vipera*. Viewed laterally it is longer, more gracile, more pointed and tapered in *Vipera*, and tends to extend further posteriorly beneath the articular condyle. *V. berus* has its hypapophysis tapered, with the tip acute and curved slightly posteriorly. *V. aspis* has a distinctly broader hypapophysis, with a fairly constant width along its length. The tip is angular and obliquely shouldered. In *Natrix* it is more rounded at its tip, generally wide along its length and more bulky. The hypapophysis is slightly more pointed in *N. maura*, but this alone does not appear to be a great enough distinction for diagnostic purposes. The shape of the prezygapophyseal processes aids diagnosis. In *N. natrix*, these are almost directed laterally and do not reach the anterior edge of the prezygapophyses. In *N. maura*, they are angled anterolaterally and reach at least to the anterior edge of the prezygapophyses. *E. longissima, C. viridiflavus* and *C. austriaca* have no hypapophysis. In place of this, *C. austriaca* has a low, wide haemal keel. *C. viridiflavus* has a narrow, deeply laterally-indented keel. This only protrudes as a small bump at its posterior end, close to the articular condyle. *E. longissima* has an indistinct, narrow ridge-like keel which protrudes as an acute bump posteriorly, close to the articular condyle. It sides are slightly constricted, the ventral surface slopes posteriorly, and there is a fine ventral crista running along its length.

Trunk vertebrae of *Natrix* tend to have a higher, more vaulted posterior neural arch than in *Vipera* (Markert, 1975; Holman, 1991). Rage and Ford (1980) noted that snake vertebrae are typically less vaulted towards the posterior end of the vertebral column. Thus, an anterior trunk vertebra of *Vipera* may appear similar to a posterior trunk vertebra of *Natrix*, using only this character and it must be used in conjunction with other diagnostic criteria. Anterior trunk vertebrae also have a more rounded neural arch, becoming lower and slightly angular in more posterior vertebrae. *C. viridiflavus* and *C. austriaca* vertebrae are vertically compressed.This is most apparent from posterior view, as the neural arch is almost flat-topped and shouldered laterally, with shallow-sloping sides. *C. viridiflavus* can be separated from *C. austriaca* as it has longer and more acute prezygapophyseal processes, which are slightly anterolaterally directed, and its neural spine is only slightly longer than it is high (Szyndlar, 1991). The neural spine in *C. viridiflavus* is long and low, with a deeply undercut anterior end. *E. longissima* vertebrae are shorter than the other taxa, and wider than they are long. The posterior neural arch is not arched, but has fairly straight sloping slides. The neural spine is well-rounded and the prezygapophyseal processes are short.

The neural spine is similar in height and shape in *Natrix* and *Vipera*, but is normally more undercut at its ends in *Natrix* (i.e. concave rather than almost straight) (Hallock *et al*, 1990; Holman, 1991). Markert (1975) also noted that the zygapophyses (articular surfaces) in*Vipera* tend to be tilted along a linear axis, but they are flatter in *Natrix*. This is, however, not as obvious as the differences in height (vaulting) of the neural arch.

The upper edges of the neural arch are known as the zygosphene (anterior end) and the zygantrum (posterior end). These provide an additional pair of small articulations with the adjacent vertebrae, to improve the strength of the vertebral column. The former is produced into a zygosphene lobe (Rage and Ford, 1980) and can have a fairly distinctive shape, though it is difficult to derive firm diagnostic information from this. The zygantrum is typically indented sharply. In *C. viridiflavus* and *C. austriaca,* the zygosphene is straight, with hooked corners, but in *Vipera* and *Natrix*, it has a sinuous margin. *E. longissima* has a more robust zygosphene, with broad, rounded lateral lobes. In all the species studied here, the zygantrum is undercut by recesses which are contained by the postzygapophyseal articulations beneath. The degree of vaulting in the posterior neural arch is reflected in the shapes of these recesses.

The prezygapophyseal processes are most useful in diagnosis between species of *Natrix* (Markert, 1975; Szyndlar, 1984; Hallock *et al*, 1990; Holman, 1991). In *N. natrix* they are fairly massive and bulbous, whereas in *N. maura* and *tessellata* they are more pointed and tapered. These are subtle characters, and confident identification of fossil material should rely upon several combined characters to achieve a satisfactory degree of certainty. No specimens of *N. tessellata* have been studied, and as this species is closely related to *N. maura* (Arnold and Burton, 1978), only identifications of *N. maura/tessellata* (cf. Holman *et al*, 1990) would be safe as yet.

Caudal and sacral vertebrae

Caudal vertebrae of European colubrids and viperids possess paired ventral processes known as haemapophyses (Szyndlar, 1984). The haemapophyses are similar in character to the singular hypapophysis of the trunk vertebrae for each species. Diagnosis should nevertheless rely on a combination of characters. In addition to the ventral haemapophyses, there is a pair of wide ventrolaterally directed transverse processes known as pleurapophyses (Szyndlar, 1984). These are long, curved, fairly fragile and tapered in *Coronella* and *Vipera*, with their tips directed downwards, but there is certainly substantial variation in their size within the tail region. The pleurapophyses of *Natrix* are relatively short and more robust, but direct comparison with type material is essential here. *C. viridiflavus* has very broad haemapophyses, unlike any other species, which are widest at their tips. The pleurapophyses are straight, broad and viewed anteriorly, they appear ventrolaterally directed. In lateral view, they are angled strongly anteriorly, reaching well beyond the prezygapophyses. In *E. longissima* there seems to be considerable variation, including assymmetry, in the form of the haemapophyses. They are generally long, ventrolaterally directed and fairly straight.

The cloacal or sacral vertebrae are similar to the subsequent caudals, but possess an additional pair of horizontally directed processes called lymphapophyses. These are essentially fused forked ribs (Rage, 1984; Szyndlar, 1984). In *Natrix*, the superior branches of the lymphapophyses are short and robust, but the inferior ones are long and gracile. In *Coronella*, both the upper and lower lymphapophyses are fairly short and robust, but taper towards their tips. In *Vipera*, both are very thin and gracile. The lower lymphapophyses are also distinctive as they are proximally more ventrally directed than in *Natrix* and *Coronella*, bending laterally along the rest of their length. For *Natrix* and *Vipera*, the overall character of the trunk vertebra hypapophysis (i.e. spatulate in *Natrix*, pointed and gracile in *Vipera*) is mirrored in these additional processes. In *E. longissima*, the lower pair are angled posterolaterally, and extend beyond the posterior condyle. The upper pair are laterally directed, but their tips are angled downwards.

6 New herpetofaunal assemblages studied

Forty-one new herpetofaunal assemblages have been studied and described, and four published sites have been re-examined. An account is given of the previous work and existing knowledge on each site, followed by the full systematic palaeontological description of the herpetofaunal material. Information on the provenance of samples is as complete as possible and relevant section drawings are given where available. The sites have been divided into seven regions and are listed below. The locations of these and the sites already published are shown in Figure 8.1.

Southeast England

Sutton Courtenay, Oxfordshire
Cassington, Oxfordshire
Stanton Harcourt, Oxfordshire
Marsworth (Lower Channel), Buckinghamshire
Ightham Fissure, nr. Sevenoaks, Kent
Chislet, Kent
Boxgrove, West Sussex

Southwest England

Kent's Cavern (Wolf Den), Torquay, Devon
Cow Cave, Chudleigh, Devon
Tornewton Cave (Otter Stratum, Hyaena Stratum), Torbryan, Devon
Broken Cavern, Torbryan, Devon
Three Holes Cave, Torbryan, Devon
Torbryan Six Cave, Torbryan, Devon
Wookey Hole (Hyaena Den), nr. Wells, Somerset
Milton Hill Cave, nr. Wells, Somerset
Denny's Hole, Compton Bishop, Somerset
Lower Cave, Clifton, Bristol, Avon
Rogers' Cave, Symond's Yat, Wye Valley, Herefordshire

Wales

Madawg Rockshelter, Wye Valley, Gwent
Hoyle's Mouth Cave, Tenby, Dyfed
Little Hoyle Cave, Tenby, Dyfed
Potter's Cave, Caldey, Dyfed
Cathole, Gower, West Glamorgan
Pontnewydd Cave, Clwyd

Fens and East Anglia

Wardey Hill, Coveney, Lincolnshire

Little Duke Farm, Deeping St. Nicholas, Cambridgeshire

Leaves Lake Drove, Pinchbeck, Cambridgeshire

Outgang Road, Market Deeping, Lincolnshire

Third Drove, Gosberton, Lincolnshire

Mornington House, Gosberton, Lincolnshire

Chopdike Drove, Gosberton, Lincolnshire

Hay Green, Terrington St. Clement, Norfolk

Ingleborough Farm, West Walton, Norfolk

Rose Hall Farm, Walpole St. Andrew, Norfolk

Deeping St. James, Norfolk

Northern England

Pin Hole Cave, Creswell, Derbyshire

Robin Hood's Cave, Creswell, Derbyshire

Whitemoor Channel, Bosley, Cheshire

Scotland

Badger Cave, Creag nan Uamh, Sutherland, Highland Region

Bone Cave, Creag nan Uamh, Sutherland, Highland Region

Smoo Cave, Durness, Sutherland, Highland Region

Ireland

Plunkett Cave, Keishcorran, Co. Sligo

Dermot and Grania's Bed, Bricklieve Mountains, Co. Sligo

Pig Cave, Bricklieve Mountains, Co. Sligo

6.1 Southeast England

SUTTON COURTENAY, OXFORDSHIRE

This site is a gravel pit (NGR SU518923) near the village of Sutton Courtenay. Commercial gravel extraction (Amey Roadstone Company) from the Devensian floodplain terrace of the Thames has for several years produced numerous large vertebrate remains. Regular collection of bones and stone tools has been carried out since c.1993, mainly by B. Eeles and J. Wallace (Abingdon Archaeology Unit). The site is mentioned by Briggs *et al* (1985) with reference to its context in the Upper Thames terrace sequence. The results of interdisciplinary research on the site are as yet unpublished, but there is abundant scope for vertebrate (mammal, amphibian, bird and fish), plant, molluscan, beetle, ostracod and lithic studies. No site plans or sections are currently available.

Study has centred on an area known as Site 2, close to the southwestern corner of the pit, adjacent to Didcot Power Station. A layered sequence of organic-rich deposits, of fluviatile origin, was exposed near the base of the gravel sequence during 1993-4. The stratigraphy was, Oxford Clay at the base overlain by around 1m of fine pale grey shelly silty fine sand. Towards the bottom of this unit, there was a thin layer (about 5cm thick) consisting of plant remains with abundant shells and small vertebrate bones. Its upper and lower boundaries are sharp. This is unconformably overlain by about 3m of cold-stage gravels, which are in turn capped by about 1m of Holocene alluvium. Large mammals from the overlying gravels have been abundantly collected and include mammoth, woolly rhinoceros and hyaena. These remains are mainly in the possession of B. Eeles, and include numerous rhinoceros teeth and fairly complete skulls of rhinoceros and hyaena. This mammal assemblage is clearly of the 'Coygan-type' which Currant and Jacobi (1997) assigned to Oxygen Isotope (O.I.) Stage 3 (Middle Devensian). Artefacts are also known from the gravels.

Samples from the underlying grey silty sand at Site 2 were wet-sieved through a 500μm sieve, and yielded rich molluscan assemblages. Because of the fine nature of the sediment, sieving greatly reduced the volume of the sample. The species list from a 1kg sample of the grey sand is as follows:

Valvata piscinalis
Lymnaea truncatula
Lymnaea peregra
Lymnaea palustris
Planorbis planorbis
Anisus vortex
Anisus leucostoma
Bathyomphalus contortus
Gyraulus laevis
Hippeutis complanatus

Pisidium subtruncatum
Pisidium henslowanum
Pisidium nitidum
Pisidium obtusale
Pisidium obtusale lapponicum
cf. *Succinea oblonga*
cf. *Oxyloma pfeifferi*
Vertigo pygmaea
Vertigo genesii
Pupilla muscorum
Vallonia costata
Vallonia pulchella
Vallona enniensis
Carychium minimum
Columella columella
Trichia cf. *hispida*

This fauna has some notably 'Arctic' species in it, particularly *C. columella*. Some of the very numerous *P. muscorum* are notably rotund, approaching the alpine species *P. alpicola* in form. Perhaps the most notable element of the fauna is the inclusion of the rare cold-tolerant species *P. o. lapponicum* which Coope *et al* (1961) recorded from Upton Warren. Dance (in Coope *et al*, 1961) discussed the implications of this form which is considered to be an Arctic subspecies, noting its presence at Nazeing and several other Lateglacial sites in Britain. Some of the Sutton Courtenay specimens are very broadly inflated and there is no doubt that they are of the Arctic form. Others are less tumid and might only be considered as *P. obtusale*. This supports a similar palaeoclimatic reconstruction to that at Upton Warren.

A 3kg sample specifically from the thin layer of vegetable matter near the botton of the grey sand was wet-sieved down to a residue of 850g and estimated to contain c.10,000 mollusc shells. Most notably, it produced five additional species. In particular, large numbers of *Bithynia tentaculata* were present, with lesser numbers of *Sphaerium corneum, Pisidium amnicum, Pisidium milium* and *A. fluviatilis*, indicating a well-vegetated flowing water body.

Independent analyses of large volumes of material were also undertaken by B. Eeles (pers. comm. 1993), who counted over 16,000 shells and recorded eleven additonal species: *Valvata cristata, Lymnaea stagnalis, Planorbis carinatus, Armiger crista, Planorbarius corneus, Acroloxus lacustris, Cochlicopa lubrica, Trichia striolata, Cepaea nemoralis, Cernuella virgata* and *Ena obscura.*

It is interesting to note that Coope *et al* (1961) observed great differences in the molluscan faunas between their Bands 2 and 3, with elements in Band 2 being decidedly stunted and including the Arctic *P. o. lapponicum.* At Sutton Courtenay, the samples from Site 2 show similar

differences up the profile. Whereas the bulked sand sample contained 26 species including the cold-tolerant *P. o. lapponicum* and *C. columella* but lacked *B. tentaculata*, the assemblage from the thin organic band below produced abundant *B. tentaculata, S. corneum, A. fluviatilis* and other cold-intolerant species. *Ena obscura* is a notable thermophile, becoming scarcer in the northern areas of its range, reaching southern Ireland, Scotland and southern Scandinavia as far as 60°N (Kerney and Cameron, 1979. It may be significant that its range has some similarities with that of *B. calamita*, which has been recovered from the same deposits at Sutton Courtenay (see below). The total number of molluscan species from the grey silty sands now stands at forty-two. As stated above, this is likely to comprise a mixed assemblage, with thermophilous elements from the thin band rich in vegetable matter, and notably Arctic species from the overlying sand. This seems to indicate that deposition of the organic band took place under mild temperate conditions, but that the sands above saw the onset of cold conditions. The stratigraphic boundary between them is sharp and supports the notion that climatic deterioration was quite rapid.

Numerous beetle remains, ostracods, seeds and fruits are also present in the samples analysed, and are particularly concentrated in the organic band. Representatives have been picked though none are as yet identified. Several species of moss have been identified by C.R. Stevenson (B. Eeles, pers. comm., 1993): *Polytrichum juniperinum, Drepanocladus revolvens, Calliergon giganteum, Bryum ?pseudotriquetrum* and *Scorpidium scorpioides*. Abundant small vertebrate remains, including numerous fish bones, vole skulls, mandibles and teeth and bird bones were also recovered, but these are also unidentified at present. An immature polecat humerus, with its epiphyses missing, from sample SC2 #3 does not appear to be identical to recent *Mustela putorius,* and might belong to the extinct Pleistocene species *M. robusta* (cf. Newton, 1894).

The only amphibian bone from any of the samples is an ilium of *B. calamita* from the organic band. The ilium has its ala mostly missing, but other features such as the tuber superior are perfectly preserved. Thus, its delicate nature and the pristine condition of the associated molluscs mean that they cannot have travelled far. The combination of the different lines of evidence presenting themselves at Sutton Courtenay potentially makes this one of the most important Middle Devensian sites in Britain.

Systematic palaeontology

Bufo calamita

Material. Sample SC2 #3. One partial left ilium.

Remarks. The ala is missing and part of the lower corpus is missing (see Figure 6.16f)). The tuber is sharply pointed, with straight sides and a well-defined medial ridge. The anterior side has a smaller radiating ridge. The lateral face rises very smoothly, giving a neat pyramidal appearance in dorsal view. The bone is less than 4 mm long, and is a very unusual and notable find in the circumstances. The perfect preservation of the tuber, whilst the ala is broken, is notable. It

may be that predator breakage is involved, cf. examples observed by Pinto Llona and Andrews (1996, 1997). Interestingly, the polecat (also found in sample SC2 #3) is known to be a taker of toads (Gleed-Owen, 1996b).

CASSINGTON, OXFORDSHIRE

This site (NGR SP475108) was a commercial gravel pit operated by ARC Limited, situated between the villages of Cassington and Yarnton, on the floodplain terrace of the River Thames, 6km northwest Oxford (see Figure 6.1a). The site was quarried in four phases, the most important exposures being revealed during Phase 2 (1990-1992), and is now permanently flooded. Maddy *et al* (1998) detailed findings from observations, surveys and section sampling carried out between 1992 and 1994. Beneath the laterally extensive Devensian cold stage gravels of the area, organic channel fill deposits of a temperate nature were observed at various locations in the site.

The land surface lies at 59m above OD, about 1m above the present River Thames (Maddy *et al*, 1998). The lithology (see Figure 6.1b) of the area consists of around 3-4m of fluvial deposits, which Maddy *et al* divided into five facies types, themselves overlain by 1m of Holocene alluvium. The underlying bedrock is Oxford Clay. Facies Association A comprise crudely stratified well -sorted limestone gravels. It forms an almost continuous basal layer across the site, up to 1m thick, and lies upon an eroded bedrock surface. Association B exists as isolated scour hollows and channel fills on the Oxford Clay, and as laterally persistent units of organic sands and silts within the lower 1m of the gravel sequence. These are believed to have been deposited during a temperate Substage of Oxygen Isotope Stage 5, post-dating the Ipswichian (Last) Interglacial (Maddy *et al*, 1998). Association C comprises discontinuous beds of medium to fine sand, up to 1m in thickness. They have an erosional base and form channel fills with a higher width-depth ratio to that of the organic units in Association B. Association D is predominantly coarse gravel, up to 2m thick, forming planar beds across the whole site. Association E is a medium to fine gravel, around 1.5m thick, and is less continuous than Association D.

Numerous large vertebrate remains have been collected from the Devensian gravels, including mammoth, reindeer, bison, wolf and woolly rhinoceros (Scott and Hardaker in Maddy *et al*, 1998). This assemblage appears to be a Coygan-type fauna which Currant and Jacobi (1997) assigned to Stage 3, the Middle Devensian. At one area of the site, towards the base of the sequence, a spread of partly-associated reindeer remains were uncovered (Scott and Hardaker in Maddy *et al*, 1998). Reindeer was abundant in the Early Devensian Banwell-type faunas of Currant and Jacobi (1997), and as it lacks mammoth and woolly rhinoceros, this basal part of the gravel sequence at Cassington could be Early Devensian in age.

Arboreal pollen spectra from the temperate units are dominated by pine, but also yielded small amounts of oak, lime, spruce, birch, hornbeam, ash and alder (Scaife in Maddy *et al*, 1998). Other taxa include the shrubs juniper and hazel, heaths *Erica* and *Calluna*, and the halophyte *Plantago* cf. *maritima* associated with declining pine higher up. Wetland environments are evidenced by dominant Cyperaceae and aquatics are represented by *Pediastrum*. The 'thoroughly temperate' coleopteran fauna indicates a wide range of environmental suites in the vicinity, from dry sandy habitats to various swampy, riparian and aquatic environments (Coope in Maddy *et al*, 1998). The temperate assemblage from Sample B5 has its northern limits restricted to

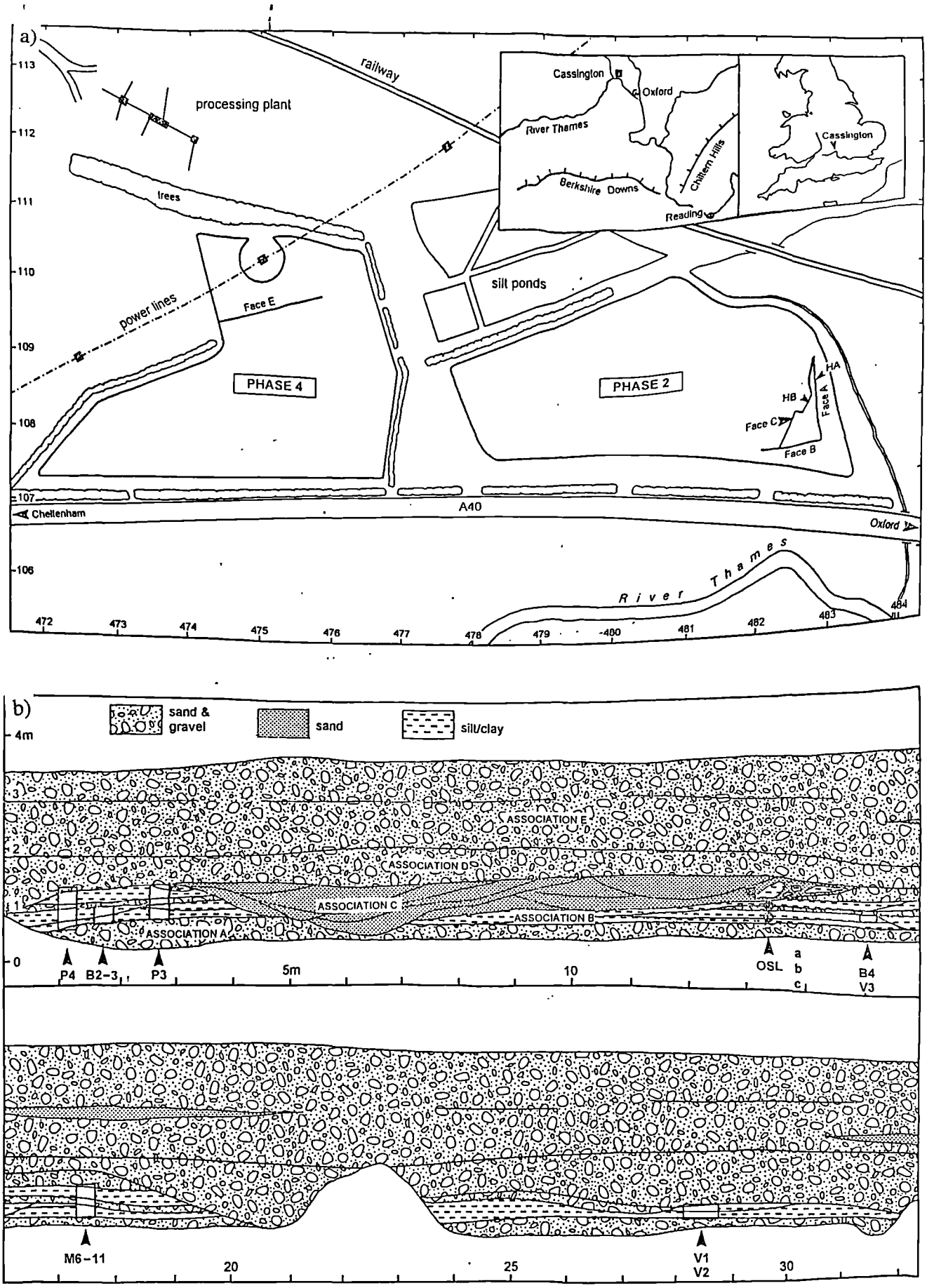


Figure 6.1 : Cassington, Oxfordshire: a) Location and plan; b) Lithostratigraphic section (after Maddy *et al*, 1998).

southernmost Sweden today. The predominantly fluvial molluscan assemblages indicate a regional climate that was 'not much different from that of the present day', with *Vertigo pygmaea* not reaching further north than 62°N today (Keen in Maddy *et al*, 1998). Fish species include dace, bleak, three-spined stickleback and gudgeon, with the most thermophilous of these (gudgeon) only reaching southern Sweden today (Parfitt in Maddy *et al*, 1998).

During a visit in June 1993, two organic layers were exposed near the bottom of the Devensian gravels in Phase 2, separated vertically by about one metre. A sample (CASS 1) from the upper layer produced an array of fairly fragmentary herpetofaunal material. According to Maddy (pers. comm.), this organic deposit is equivalent to 'Association B' of Maddy *et al* (1998) (see Figure 6.6.1b). The resulting assemblage of small bones comprises only of anuran remains, and most are not identifiable to species. However, the following herpetofaunal assemblage was identified: *B. bufo, R. temporaria, Rana* sp. (brown frog), *Rana* sp. (green frog), *Rana* sp., Anura indet. (Gleed-Owen, 1998). The sample is called 'CASS 1'. The bones are currently in the author's possession, but will be donated to the NHM in due course. Each bone has been individually numbered in the interim.

A 2kg sample was also taken in 1994 from a shelly band within the 1m layer of Holocene alluvium overlying the Devensian gravels. This was located close to the northwest end of Phase 4 of the quarry. The sample produced abundant freshwater molluscs (D.H. Keen, pers. comm.), and a single bone of *Rana* sp. The sample is referred to as 'CASS Holocene Alluvium Nov '94' below.

Systematic palaeontology

Bufo bufo

Material. CASS 1/13. One sphenethmoid.

Remarks. This is very short and wider than it is long, with a sharply indented posterodorsal margin. The anterolateral edges has rounded notches, charatceristic of *B. bufo.*

Rana temporaria

Material. CASS 1/5. One left ilium. CASS 1/3. One left humerus.

Remarks. The incomplete ilium is of a juvenile (c.25-30mm long). Its tuber is low and rounded, the vexillum is very low, and the junctura is relatively thin. The humerus is of a mature male frog, and has strong medial and lateral crests. These are directed posteriorly, as is characteristic of brown frogs. Both cristata extend the full length of the shaft, converging only towards the top, as in *R. temporaria.*

Rana sp. indet. (brown frog)

Material. CASS 1/4. One right ilium. CASS 1/11. One right tibiofibula. CASS 1/17. One trunk vertebra. CASS Holocene Alluvium Nov '94. One trunk vertebra.

Remarks. The ilium is incomplete, with the vexillum and top of the tuber missing,

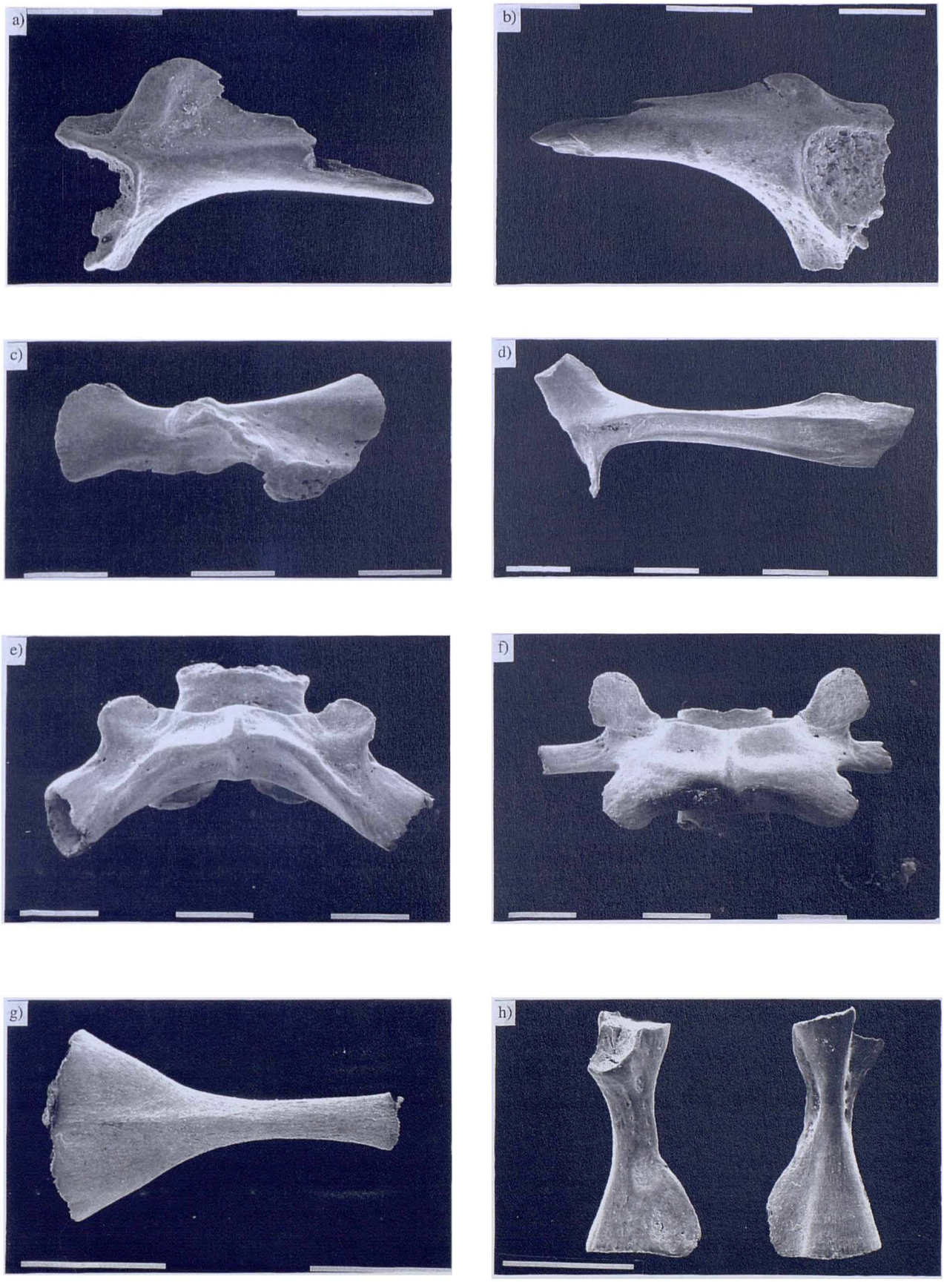


Figure 6.2: Amphibian remains from Cassington (sample taken 11.6.93): a) right ilium (lateral view) of *Rana* cf. *ridibunda*; b) left ilium (lateral view) of *R. temporaria*; c) second digit metacarpal from left manus of mature male *Rana* sp. - brown frog; d) left squamosal (medial view) of *Rana* sp. - green frog; e) sacrum (dorsal view) of *Rana* sp.; f) trunk vertebra (dorsal view) of *Rana* sp.; g) omosternum (dorsal view) of *Rana* cf. *ridibunda*; h) anuran tadpole scapulae? (dorsomedial and ventrolateral views).

preventing specific determination. The corpus is also incomplete, but the junctura is relatively thin, as is characteristic of brown frogs. The right tibiofibula is in two pieces, clearly broken post-excavation. It is relatively straight, with more slender diaphyses than in green frogs. The trunk vertebra has a weaker transverse dorsal ridge than in green frogs, and only a low neural spine. This is highest at its mid-point and not produced into a posteriorly-directed crest, as in the green frogs. CASS Holocene Alluvium Nov '94. The trunk vertebra lacks any neural crest and its anterior neural arch is not indented. It almost certainly belongs to a brown frog (probably but not certainly *R. temporaria*).

Rana sp. indet. (cf. green frog)

Material. CASS 1/2. One right ilium. CASS 1/22. One omosternum. CASS 1/6. Left squamosal.

Remarks. CASS 1/2. The ilium is incomplete, with much of the corpus and ala missing. The tuber is high and steep, with a well-defined lateral facet, which is protrusive and has no surface ridges. The specimen is only 3mm long, and probably belonged to a tadpole. In such a small specimen, it would be unwise to attempt a more specific diagnosis. CASS 1/22. The omosternum is relatively broad and thin, with a slightly convex dorsal surface, and an almost equally concave ventral surface. It has no linear medial crest and also matches more closely with *R. ridibunda* than the other two green frog species. CASS 1/6. The squamosal is incomplete, with both the anterior and posterior processes missing. The base of the shaft however is angular not rounded, in a way almost always characteristic of green frogs.

Rana sp. indet.

Material. CASS 1/8. One sacrum. CASS 1/1. One male left II metacarpal. CASS 1/7. One left and one right radioulna. CASS 1/20. One left fibulare. CASS 1/25. One left squamosal. CASS 1/14. One left ilium. CASS 1/18. One left angulosplenial.

Remarks. The sacrum has a strong transverse dorsal ridge, and a strong neural spine, together forming a cruciform relief. This is not depressed anteriorly, and the prezygapophyses are widely spaced, therefore its form is more akin to the green frogs, or possibly *R. arvalis*, than to *R. temporaria*. The proximal end of the metacarpal is missing, but it has strong nuptial tubers, of typical *Rana* form. The olecranon of the radioulnae are more posteriorly produced than in *Bufo*, and their overall form corresponds to *Rana*. The fibulare lacks its distal end, and its proximal epiphysis was broken post-excavation. The proximal end is ossified, but specific identification is not possible. The squamosal is incomplete, with its anterior process truncated and its lower arm missing, but it is still recogniseable as *Rana*. The ridge extending along its dorsal surface, onto the posterior process, is not sharp and is positioned dorsally rather than dorsolaterally. It is more likely to belong to a brown frog than to a green frog. The ilium has a fairly high tuber but is too rolled and incomplete to allow diagnosis beyond the genus *Rana*.

Indeterminate Anura

Material. CASS 1/19. Two urostyles. CASS 1/9. Nine metapodials and phalanges. CASS 1/26. Three tadpole scapulae. CASS 1/16. Vertebral fragments. CASS 1/15. Two exoccipital fragments and other assorted fragments. CASS 1/12. Two femora. CASS 1/21. One tibiale. CASS 1/15. Assorted fragments.

Remarks. This material is either too fragmentary for specific identification, or consists of undiagnostic elements. The tadpole scapulae are complete and recogniseable as such, but a lack of comparative material prevents diagnosis, even if possible. The femora are not *Bufo*, and probably also belong to *Rana*.

STANTON HARCOURT, OXFORDSHIRE

This site is within Dix Pit (NGR SP413051) and lies on Linch Hill, near the village of Stanton Harcourt, 7km west of Oxford. The site is within a large commercial gravel pit excavated by ARC Limited during the 1970s and early 1980s, and is currently operated as a landfill site by Greenways Limited. Briggs *et al* (1985) described the Stanton Harcourt Channel deposits which were exposed during the late 1970's. The current excavations, under the direction of C. Buckingham and K. Scott, have been carried out since 1990 and digging is continuing into a final season in 1998. The geology, vertebrate fauna and stone implements were discussed provisionally by Buckingham *et al* (1996), but analysis on all aspects of the geological context, biota and archaeology are continuing.

The site lies beneath the Stanton Harcourt Gravel Member of the Summertown-Radley Terrace which was deposited under periglacial conditions (Buckingham *et al*, 1996). Usually these gravels lie unconformably on Oxford Clay, but in a restricted area of Dix Pit, it is underlain by a thin bed known as the Stanton Harcourt Channel Deposits. The age of these deposits is now widely believed to be Stage 7 (Bridgland, 1994; Buckingham *et al*, 1996) and Bowen *et al* (1989) suggested that Stanton Harcourt be recognised as the type-site for the Stage 7 interglacial. The Channel trends SW-NE and fills a shallow, linear depression 60-70m wide and up to 1.5m deep, with its base at about 63.00m above OD (Buckingham *et al*, 1996). Its stratigraphy (see Figure 6.3b) consists of a complex sequence of silt, sand and gravel, frequently overlying a bed of boulders and cobbles at the junction with the Oxford Clay. Ice wedge casts often bisect the deposits, and there are various signs of periglacial disturbance particularly towards the top of the deposits.

Numerous large vertebrate remains (see Figure 6.3a) and a rich molluscan fauna, together with an abundance of wood, seeds and other organic remains give clear evidence of a riparian environment experiencing a temperate interglacial climate, probably warmer than today. An optimal but rather open interglacial woodland cover, consisting largely of oak, beech and hornbeam, is evidenced by numerous tree trunks and twigs (Buckingham *et al*, 1996). In addition, fruits and seeds are common and a list of over thirty species identified by J. Campbell includes alder, birch, blackthorn, elder and pine in a disturbed herb-rich grassland setting. Pollen preservation at the site is poor. Beetle remains identified by G.R. Coope include many species of southerly range, and suggest a climate at least as warm as today, and perhaps warmer. The assemblage does have affinities with those from Stage 5 and 9 sites but, in keeping with other Stage 7 sites, it has distinct characteristics of its own.

The large mammal fauna, identified by K. Scott, consists mainly of mammoth but includes straight-tusked elephant, bison, horse, red deer, a large deer, hyaena, lion, brown bear and a canid (possibly wolf). Most notable is the abundance of Ilford-type mammoth (small but with long tusks) in what was clearly an interglacial environment, and especially in association with straight-tusked elephant. Hippopotamus, which is typical of Ipswichian Interglacial (Substage 5e) sites, is notably missing from Stanton Harcourt and other Stage 7 assemblages. A number of *in situ*

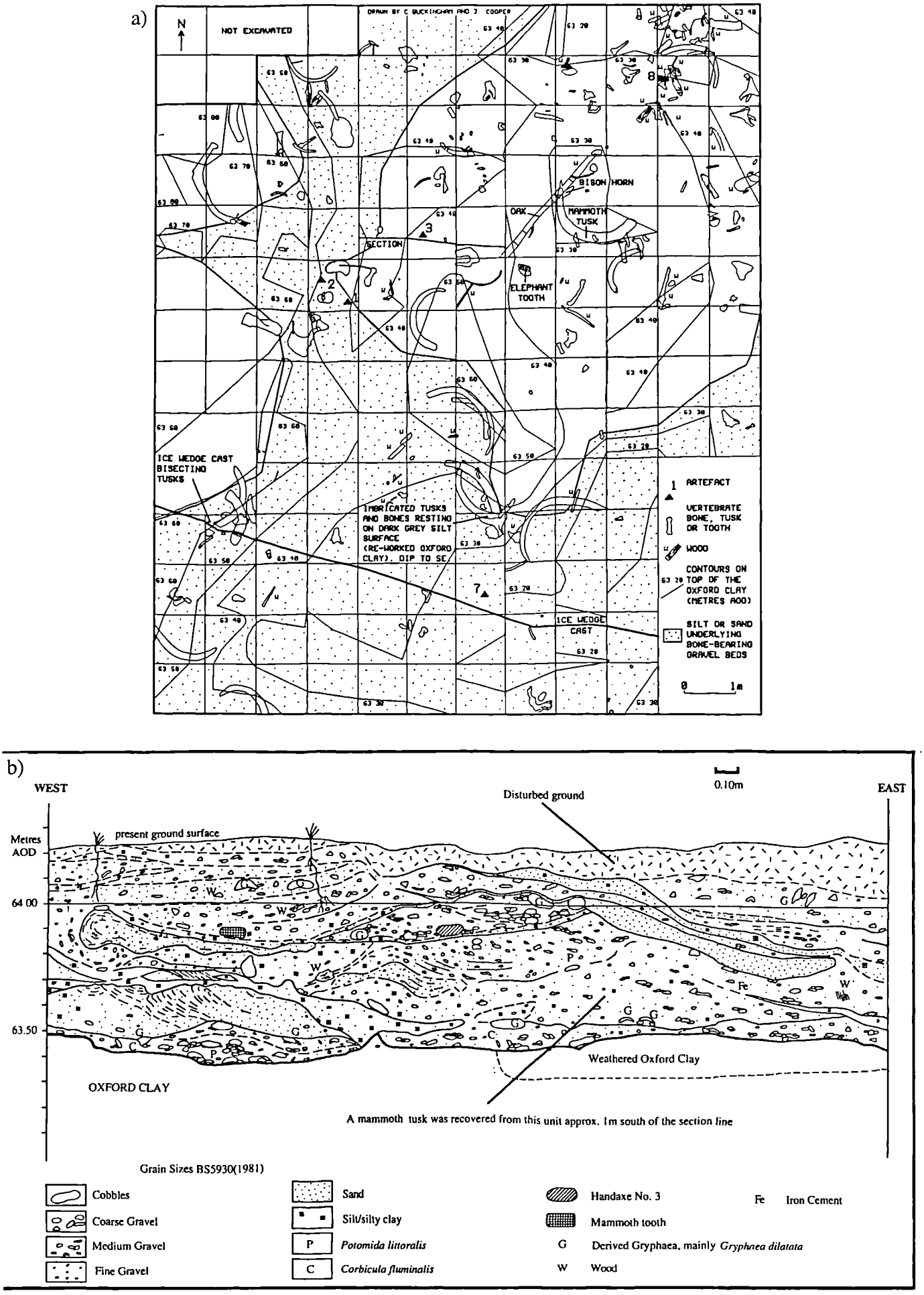


Figure 6.3: Stanton Harcourt, Oxfordshire: a) Plan of deposits, bones and other finds at Site 1; b) Lithostratigraphic section at Site 1 (after Buckingham *et al*, 1996).

Acheulian bifaces and flakes have been recovered from the channel deposits. These show various degrees of wear and none can be equivocally linked with the interglacial deposits and biota at the site (Buckingham *et al*, 1996).

The molluscan assemblage, identified by D.H. Keen and the current author is dominated by moving water species. In particular, abundant shells of thermophilous bivalves such as *Corbicula fluminalis* and *Potomida littoralis* indicate warm temperate conditions, The woodland obligate gastropod *Spermodea lamellata* supports the presence of an open but mature woodland. Eleven species of fish have been identified by B. Irving: three-spined stickleback, pike, perch, eel, bream, gudgeon, dace, chub, roach, stone loach, salmon. Eel fry travel from the Sargasso Sea to the British Isles on the Gulf Stream, indicating that its position was in interglacial mode (Irving, pers. comm. 1995). The overall assemblage is typical of the upper reaches of the Thames today.

Sixteen bulk samples of organic silt, sand and gravel, each weighing c.4-6kg, were sieved at 250 or 500μm. The residues were initially studied in order to extract molluscan remains in 1993, but all small vertebrate remains were also removed. The icthyofaunal remains identified by Irving were extracted from these samples. Each sample has produced a few fragmentary anuran remains, but they were disappointingly sparse. Most of the remains are not easily identifiable and few can be identified to species or even to genus level. There appears to be a taphonomic bias against terrestrial small vertebrates in the samples. Only a few poorly preserved microtine teeth were recovered, and the remains of amphibious species such as anurans were scant. Conversely, as described above, freshwater Mollusca were abundant and eleven fish species were identified.

The herpetofaunal list identified is as follows: *T. vulgaris/helveticus, R. temporaria, R.* cf. *temproaria, R.* cf. *arvalis/dalmatina, Rana* sp. (cf. green frog), *Rana* sp., cf. *Rana* sp., Anura indet. The bones are currently in the author's possession, but will eventually be passed to Oxford University Museum. The taxa recovered from each sample are listed in Table 6.1. The first four digits are the sample numbers, but the bones have been given additional individual numbers.

Table 6.1

#1041	cf. *Rana* sp.
#1046	cf. *Rana* sp.
#2002A	*Rana* sp.
#2002B	*T. vulgaris/helveticus, R. temporaria, Rana* sp.
#2003A	*Rana* sp.
#2003B	cf. *Rana* sp
#2007	Anura indet.
#2008A	Anura indet.
#2009	Anura indet.
#2010	cf. *Rana* sp.

#2011	*R.* cf. *arvalis/dalmatina*
#2017	Anura indet.
#4003	Anura indet.
#5001	*R.* cf. *arvalis/dalmatina*
#5004	*Rana* sp.
#5005	*R.* cf. *temporaria, Rana* sp. cf. green frog, *Rana* sp.

Systematic palaeontology

Triturus vulgaris/helveticus

Material. #2002B/17. One right frontal.

Remarks. This is under 2mm long, but still recogniseable as a newt frontal. It is probably from a larval animal, but its lateral edge is not well enough developed to determine the species from the size of its frontosquamosal process.

Rana temporaria

Material. #2002B/19. One partial right ilium.

Remarks. This consists only of part of the ala, which is vertically compressed towards its posterior end. The vexillum is broken, but is clearly very thick, as in *R. temporaria.*

Rana cf. *temporaria*

Material. #2002B/1. One left frontoparietal. #5005/4. One partial left ilium.

Remarks. The frontoparietal is almost identical to recent *R. temporaria* specimens, but the ventral endocast is different in shape. The medial edge is not noticeably serrated as in *R. arvalis* and *R. dalmatina*, and the endocast is not produced anteromedially as in *R. arvalis*. The anterior end of the pars frontalis is missing and the overall length cannot be seen. The bone is wider and with a larger endocast than in the green frogs, and probably belongs to *R. temporaria*, but a firm diagnosis cannot be given without comparison to *R. dalmatina* specimens. The ilium has its corpus and much of the vexillum missing, but the latter appears to be very thick as in *R. temporaria*. The tuber is sculpted into ridges on the lateral side, but has a relatively shallow posterior slope. There is a pronounced pre-acetabular fossa.

Rana cf. *arvalis/dalmatina.*

Material. #2011/1. One male left humerus. #5001/7. One left ilium.

Remarks. The humerus is of a mature male, and has strong medial and lateral cristata. The medial crista is straight edged, and extends high up the shaft, but is not deflected posteriorly as sharply as in *R. temporaria.* Also, the lateral crista does not extend as far up the posterior side of the shaft, as the lateral crista does. This is characteristic *R. arvalis* and *dalmatina,* but not *R.*

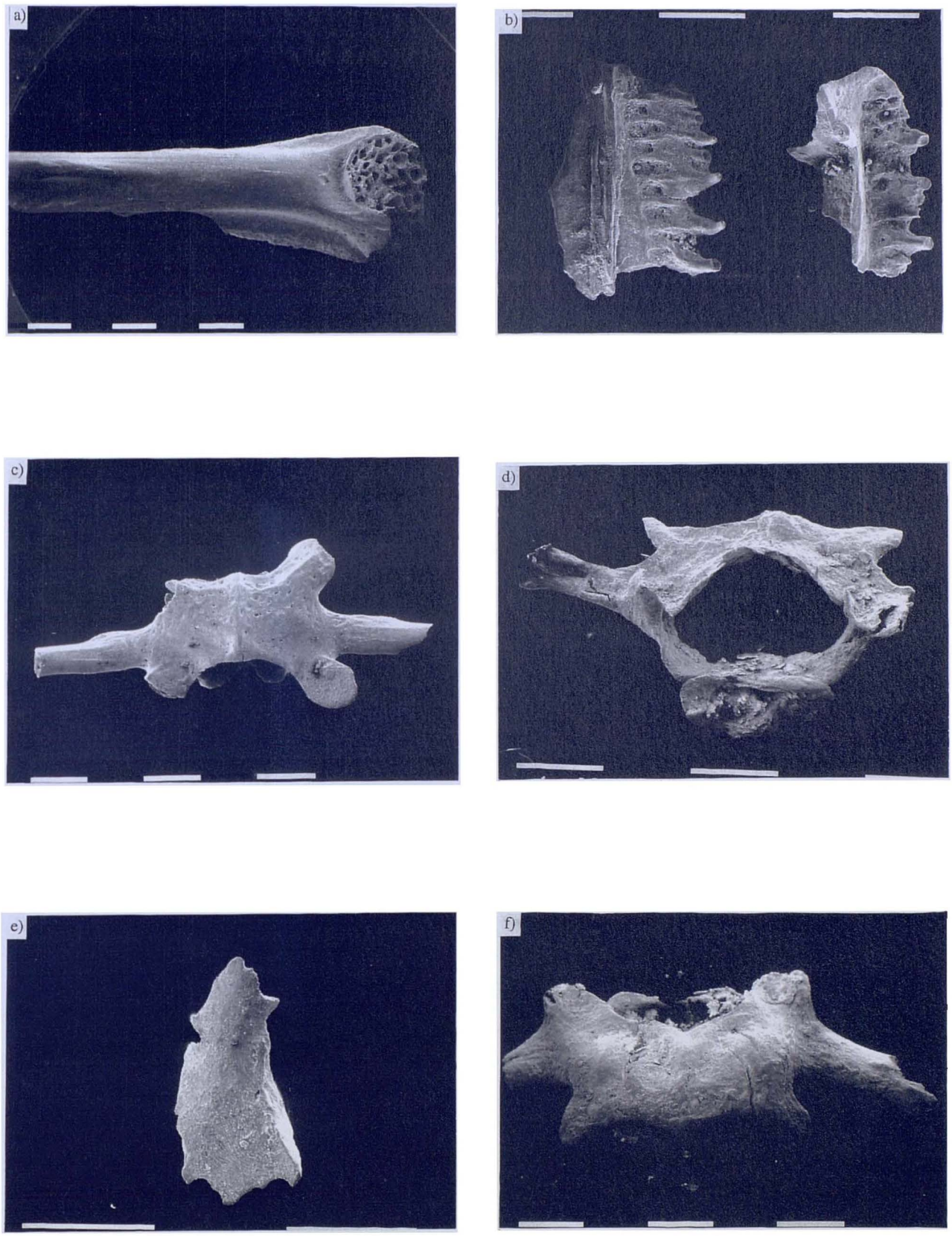


Figure 6.4: Amphibian remains from Stanton Harcourt: a) left humerus (anterior view) of male *Rana* sp. (sample 2011); b) maxillary fragments (medial view) of *Rana* sp. (samples 2010, 2002A); c) trunk vertebra (dorsal view) of *Rana* sp. (sample 2025); d) trunk vertebra (anterior view) of ?*Bufo* sp. (sample 5004); e) right frontal (dorsal view) of juvenile *Triturus* sp. (sample 2002B); f) trunk vertebra (dorsal view) of *Rana* sp. (sample 5005).

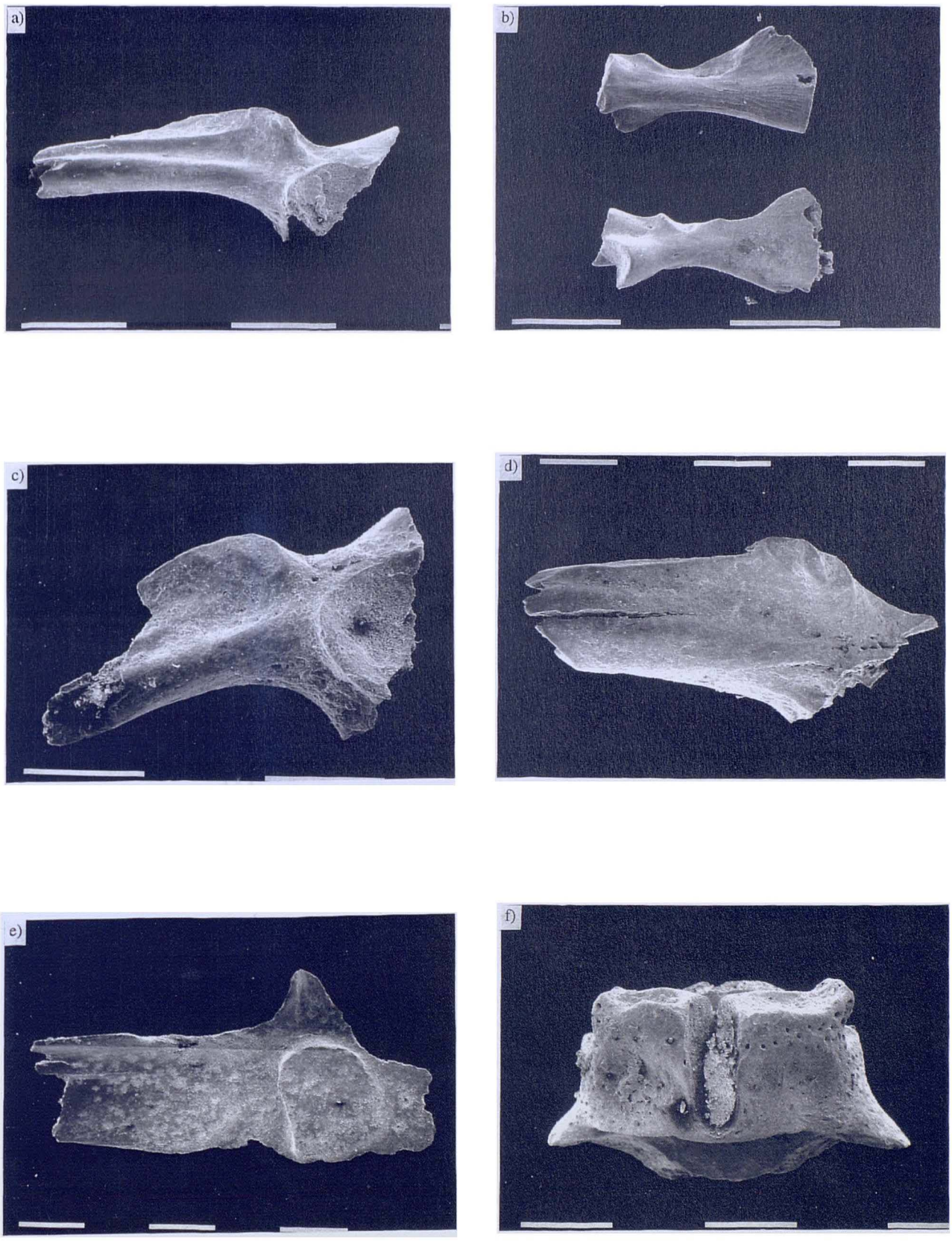


Figure 6.5: Anuran remains from Stanton Harcourt: a) left ilium (lateral view) of juvenile *Rana* cf. *arvalis/dalmatina* (sample 5001); b) anuran tadpole scapulae? (sample 2003); c) left ilium (lateral view) of *Rana* cf. *temporaria* (sample 5005); d) left ilium (lateral view) of *Rana* cf. *arvalis* (sample 5005); e) left frontoparietal (ventral view) of *Rana* sp. (sample 2002B); f) atlas vertebra (dorsal view) of *Rana* sp. (sample 1041).

temporaria. A specimen of *R. dalmatina* seen in Kraków (ZZSiD448) was very much like this one. The left ilium is minute in size, and probably came from a either tadpole or a metamorphosing froglet. The tuber has nodular rudimentary ridges on its lateral side, and the supra-acetabular fossa is deeply excavated, creating a sharp crista betwen the tuber and pars ascendens. The vexillum is high and folded medially, with the crease forming a linear ridge. Böhme (1977) noted that *R. dalmatina* has a medially deflected vexillum. The specimen seen in Kraków also had a prominent ridge along the lateral side of its vexillum.

Rana sp. indet. cf. green frog

Material. #5005/3. One left ilium.

Remarks. This ilium came from a froglet of around 30mm in length, but has already has a robust tuber and vexillum. The junctura ilioischiadica is thicker ventrally than in brown frogs. The tuber is flattened in a broad facet, which is sculpted and thickened towards it base, where it protrudes laterally. The caudal margin of the tuber is steeper, and the lateral facet is wider than in most specimens of *R. ridibunda*. The tuber matches the character of *R. esculenta* best, but the steep caudal edge and thickened basal area may also be suggestive of *R. lessonae*. It is not as bulbous as *R. lessonae* specimens seen, but juveniles would be expected to have less well developed tuber characters than adults, as discussed for recent juvenile *R. esculenta*. Unfortunately, additional comparative material would be needed to make a more conclusive identification.

Rana sp. indet.

Material. #2002A/1. One left humerus. #2002B//2. One right scapula. #2002B/3. One partial right squamosal. #2009/2. One distal phalanx. #2002B/4. One distal phalanx. #5001/2. One trunk vertebra. #5001/4. One right angulosplenial. #5001/6. One incomplete right dentary. #5004/2. One partial sacrum. #5004/6. One left angulosplenial. #5005/1. One trunk vertebra. #2002B/18. One partial left scapula. #2002A/6. One partial male second digit metacarpal. #5004/9. One partial left ilium. #5001/9. One partial trunk vertebra. #2003A/1. One incomplete left scapula.

Remarks. The humerus (Figure 6.6) is from a female, and has its distal articular surface extending further up the posterior side, and more centrally than in *Bufo*. It is identical to recent *Rana* specimens, but specific identification is not possible. The squamosal has its anterior and ventral arms missing. Its posterior arm is flared, straight edged and almost horizontal. The intact part of the vertical shaft is narrow as in the green frogs, but the dorsal part of this bone can be very variable in all species. The partial ilium (#5004/9) consists of much of the ala, with a sharp vexillum, but no corpus or tuber superior. The vexillum has a prominent crista running obliquely along the posterior part of its lateral side. The other elements would be difficult or impossible to identify to species.

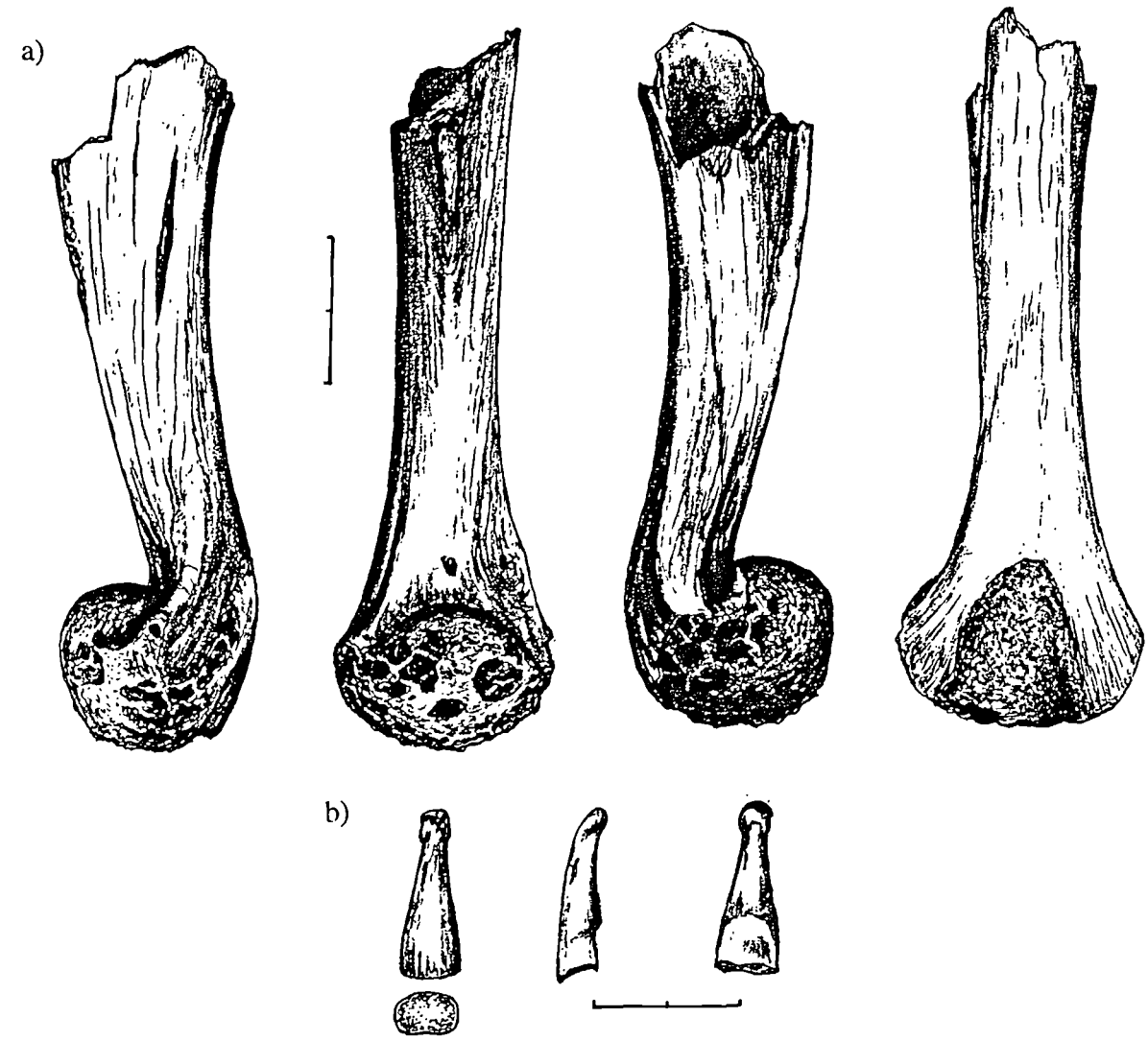


Figure 6.6: Anuran remains from Stanton Harcourt: a) left humerus of *Rana* sp. (SH2002A/1); b) distal phalanx of *Rana* sp. (SH2009/2).

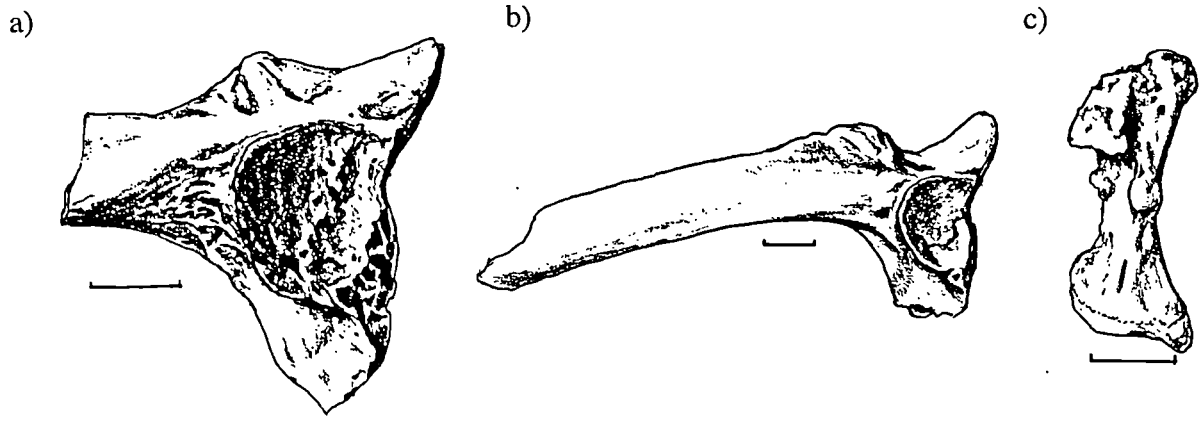


Figure 6.7: Anuran remains from Hyaena Den, Tornewton Cave: a) left ilium of *B. calamita* (TN92 252); b) left ilium of *R. temporaria* (TN92 252); c) male second digit metacarpal of *Rana* sp. (brown frog).

cf. *Rana* sp. indet.

Material. #1046/1. One indeterminate long bone (tibiale or metapodial). #1041/3. One atlas vertebra. #2010/2. One maxillary fragment. #2010/7. One metapodial. #2010/8. One metapodial. #2010/10. One trunk vertebra. #2002A/3. One metapodial. #2002A/4. One incomplete distal phalanx. #2002A/5. One maxillary fragment. #2002B/7. One left radioulna. #5001/5. One metapodial. #2003A/8. One metapodial. #2003B/1 One metatarsal.

Remarks. These elements appear to belong to *Rana*, but cannot be referred with certainty to this genus. The atlas (Figure 6.5f) has a deep linear fossa in the dorsal surface of its neural arch: a condition observed in some recent specimens of *Bufo* and *Rana*. The posterior articulation is narrow, and the overall form matches recent *Rana* closely, though specific diagnosis is not possible.

Indeterminate Anura

Material. #1041/1. One partial right radioulna. #1041/2. Partial tibiofibula. #2009/1. One right exoccipital. #2010/1. Tadpole scapula? #2010/2. One partial parasphenoid. #2010/3. One exoccipital fragment? #2010/6. Tadpole scapula? #2010/9. One metapodial. #2010/11. Tadpole scapula? #2010/12. One partial tibiale or fibulare. #2011/2. Tadpole scapula? #2011/3. Tadpole scapula? #2017/1. One phalanx. #2002A/2. One vertebral fragment. #2002B/6. One vertebral fragment. #2002B/8. One partial tibiale or fibulare. #2002B/9. Two tadpole scapulae? #2002B/10. One partial coracoid. #2002B/11. One phalanx. #2002B/12. One tadpole scapula? #2002B/14. One vertebral fragment. #5001/8. Two vertebral fragments. #5004/3. One right exoccipital. #5004/5. One left exoccipital. #5004/7. One trunk vertebra (very corroded). #5004/8. One metatarsal. #4003/1. One partial metapodial. #4003/2. One partial metapodial. #2002B/20. Three vertebral fragments. #2008A/3. One vertebral fragment and two indeterminate appendicular fragments. #2010/14. One tibiofibula. #5001/10. Three vertebral fragments. #2003A/2-7. Six tadpole scapulae? #2003A/9. One partial phalanx or metapodial. #2007/1. One vertebral fragment. #2007/2. One vertebral fragment. #2007/3. One metapodial or phalanx. #2008A/2. One tadpole scapula? #2007/4. Five indeterminate vertebral fragments and appendicular elements.

Remarks. These bones are too fragmentary to allow identification to genus, especially as comparative material has not been seen for some families. The radioulna (#1041/1) has its olecranon fairly truncated, which is more usual in *Bufo*. The tibiofibula (#1041/2) is flattened and the mid-shaft region is broad, as in *Bufo*. The parasphenoid (#2010/2) is very thin and has none of its extremities intact, but there are sharp cristata on its ventral side. The minute bones referred to as tadpole scapulae have the rudimentary form of anuran scapulae, with a double proximal articulation and a flared distal part. There are at least two forms here, and study of anuran larval osteology may be worthwhile to enable a better diagnosis. The partial tibiales or fibulares (#2010/12, #2002B/8) each have wide and rounded epiphysis, but a very constricted shaft, apparently not belonging to *Bufo* or *Rana*. The tibiofibula (#2010/14) is minute and slender, but broad, and may not be *Rana*.

MARSWORTH (LOWER CHANNEL), BUCKINGHAMSHIRE

Separate channel deposits in the Pitstone no. 3 quarry (NGR SP933144), at College Farm near the village of Marsworth, represent two distinct interglacial events (Green *et al*, 1984). The Upper Channel produced a typical Ipswichian mammal fauna, including hippopotamus, bison, giant deer, straight-tusked elephant and narrow-nosed rhinoceros. The Lower Channel yielded much more diverse fossil material, including molluscs, ostracods, beetles, pollen, plant macrofossils and vertebrates (Green *et al*, 1984). Large mammals include wolf, brown bear, lion, mammoth, a horse, an ass, indeterminate bovids and deer. Notably, it also yielded *M. oeconomus* which is known from other Stage 7 sites, but is absent from those of Ipswichian age (Currant, 1989; 1996). The associated botanical evidence suggests a herb-rich grassland, with low arboreal pollen indicating a limited woodland cover (Green *et al*, 1984). Land Mollusca include shade/woodland obligates *Azeca goodalli, Discus rotundatus* and *Clausilia bidentata.* Samples of travertine deposit from the Lower Channel were U-Th dated to 170-140 kA BP, suggesting deposition within early Stage 6. They contained a molluscan fauna indicative of temperate woodland, probably representing the latter part of an interglacial in Stage 7 interglacial or a temperate episode in early Stage 6 (Green *et al*, 1984; Jones and Keen, 1993).

Two pieces of the dated tufa, provided by A. Baker, were examined as they apparently contained anuran remains. These remains, of *Rana* sp. brown frog, *Rana* sp. and Anura indet., are described below. This material may correlate with Substage 7a, i.e. the (possibly cooler) latter half of the Stage 7 interglacial.

Systematic palaeontology

Rana sp. indet. (brown frog)

Material. 'Tufa piece #2'. One partial left scapula.

Remarks. The scapula has been broken where it protruded from the piece of tufa. Its articular surfaces and strong dorsomedial ridge are diagnostic of a brown frog species.

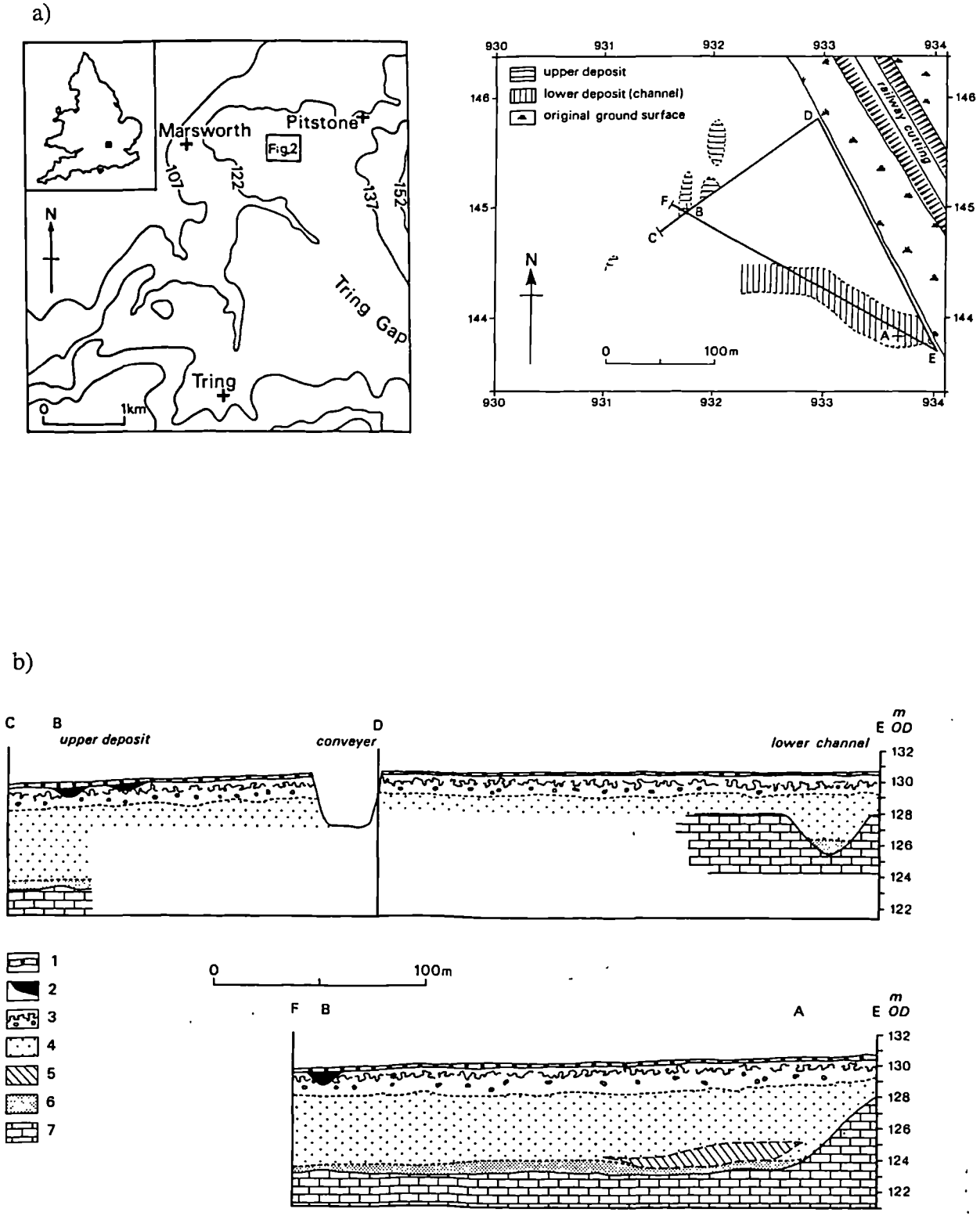
Rana sp. indet.

Material. 'Tufa piece #1'. One right humerus (female).

Indeterminate Anura

Material. 'Tufa piece #2'. One humeral shaft.

Remarks. Adjacent to the scapula, there is an exposed cross-sectional outline of a humeral shaft which may be associated with it, and is probably also *Rana*.. Its anterior crista (crista ventralis of Gaupp, 1896) is visible, but not enough to enable diagnosis to genus with certainty.



Sections in Pitstone no. 3 quarry, Marsworth. 1, Topsoil; 2, upper deposit; 3, Coombe Rock with involutions; 4, chalk muds with waterlaid sand and fine gravel; 5, organic muds; 6, fossiliferous gravelly sand; 7, Lower Chalk.

Figure 6.8: Marsworth, Buckinghamshire: a) Location and plan; b) Transverse and longitudinal sections through channel deposits (after Green *et al*, 1984).

IGHTHAM FISSURES, nr. SEVENOAKS, KENT

This site was situated in the valley of the River Shode, close to the village of Ightham, near Sevenoaks in Kent. The exact location is not reported by Newton (1894) who first drew attention to the vertebrate fauna collected by Mr. W. Lewis Abbott. The geological setting is Lower Greensand, with lithified bands locally known as Kentish Rag, in which fluvial erosion has created cambered valley sides and numerous gulleys and fissures (Newton, 1894). One such fissure contained a Late Pleistocene bone-rich infill. Though no full-scale excavations took place, vertebrate remains were collected by Abbott, over a long period towards the end of the 19th Century. Newton (1894) described a large mammalian fauna including mammoth, woolly rhinoceros, reindeer, horse, spotted hyaena, brown bear, arctic fox, an extinct polecat, collared lemming, arctic lemming, red deer and roe deer. The fauna contains both a typical Devensian cold fauna and interglacial elements, and is evidently composite.

Newton also described herpetofaunal material from this site, but seems to have misidentified *B. calamita* as *B. bufo*. Holman (1985) described the full herpetofaunal assemblage and discussed the age of the sediments. The deposits are thought to have covered most of the Devensian, though the herpetofaunal remains apparently date to the Early Holocene (Holman, 1985). The material is held at the NHM. Though this material has already been described, in the light of the current study, it was considered necessary to re-examine the ilia of *B. calamita*. The previous identifications are supported for all of the ilia and a systematic account is given below.

Systematic palaeontology

Bufo calamita

Material. NHM: R10173. Four left and six right ilia. NHM: R10176. Five left and six right ilia.

Remarks. NHM: R10173: These all have quite well defined tubers, in excellent condition. Some have very sharp apices, and one has a tiny recurved 'barb' at its apex. One or two have a slight concavity in both slopes of the tuber, as described earlier. One tuber leans slightly to the posterior. The ilia are generally quite small and are possibly from immature animals. The diagnostic criteria of the pars descendens and alae are not particularly well-developed, but all ten ilia possess characteristic tubers, which identify them as *B. calamita*. NHM: R10176: All have very clearly pointed tubers. Several have wide and angled pars descendens, two in particular have a very prominent spina pelvis anterior. Most are 16-22mm in length, complete and unbroken. Overall, '*calamita* blades' were not very prominent or diagnostic. All the ilia had easily diagnostic tubers.

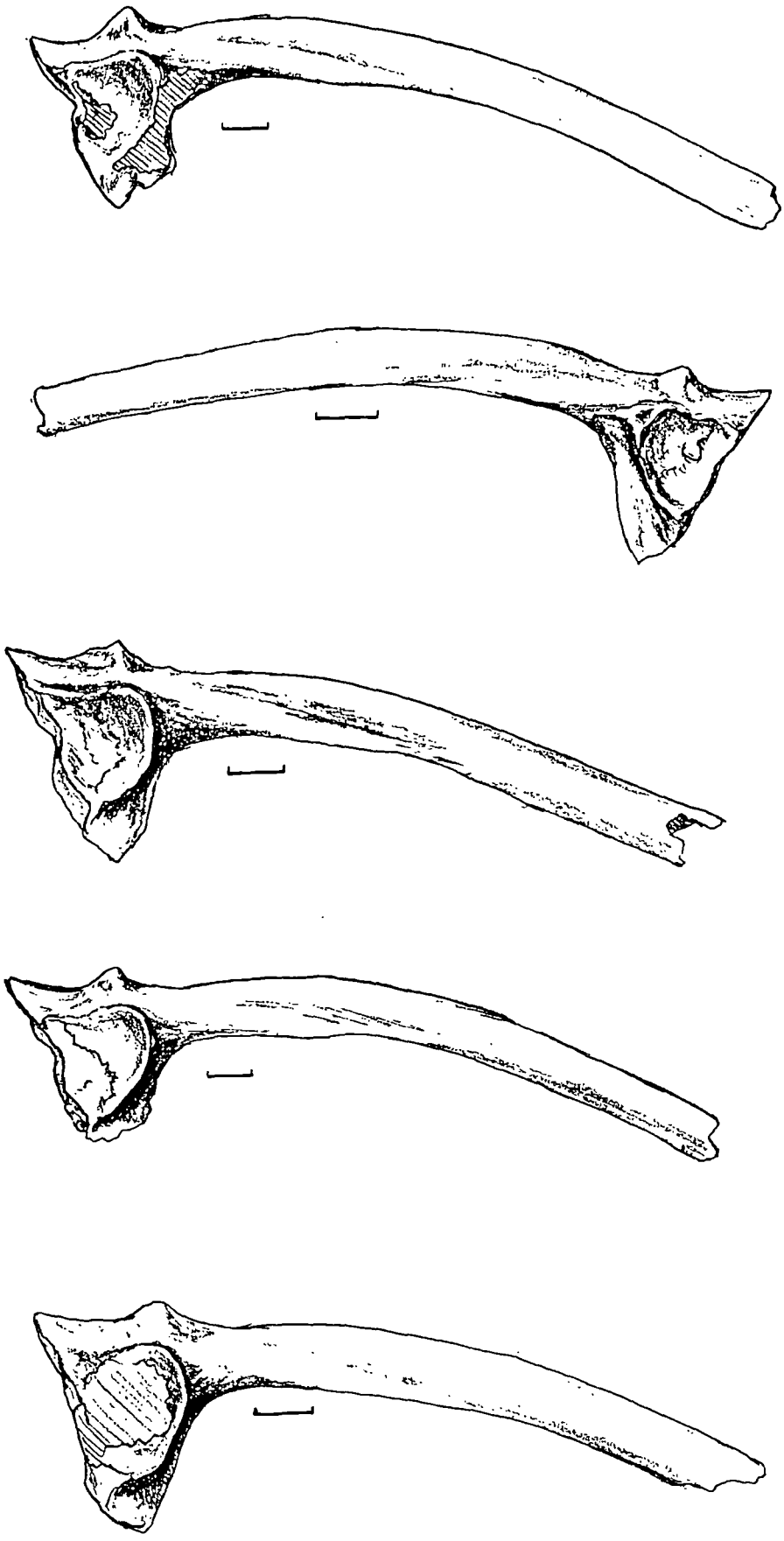


Figure 6.9: *B. calamita* ilia from Ightham fissure, Kent (BMNH: R10176).

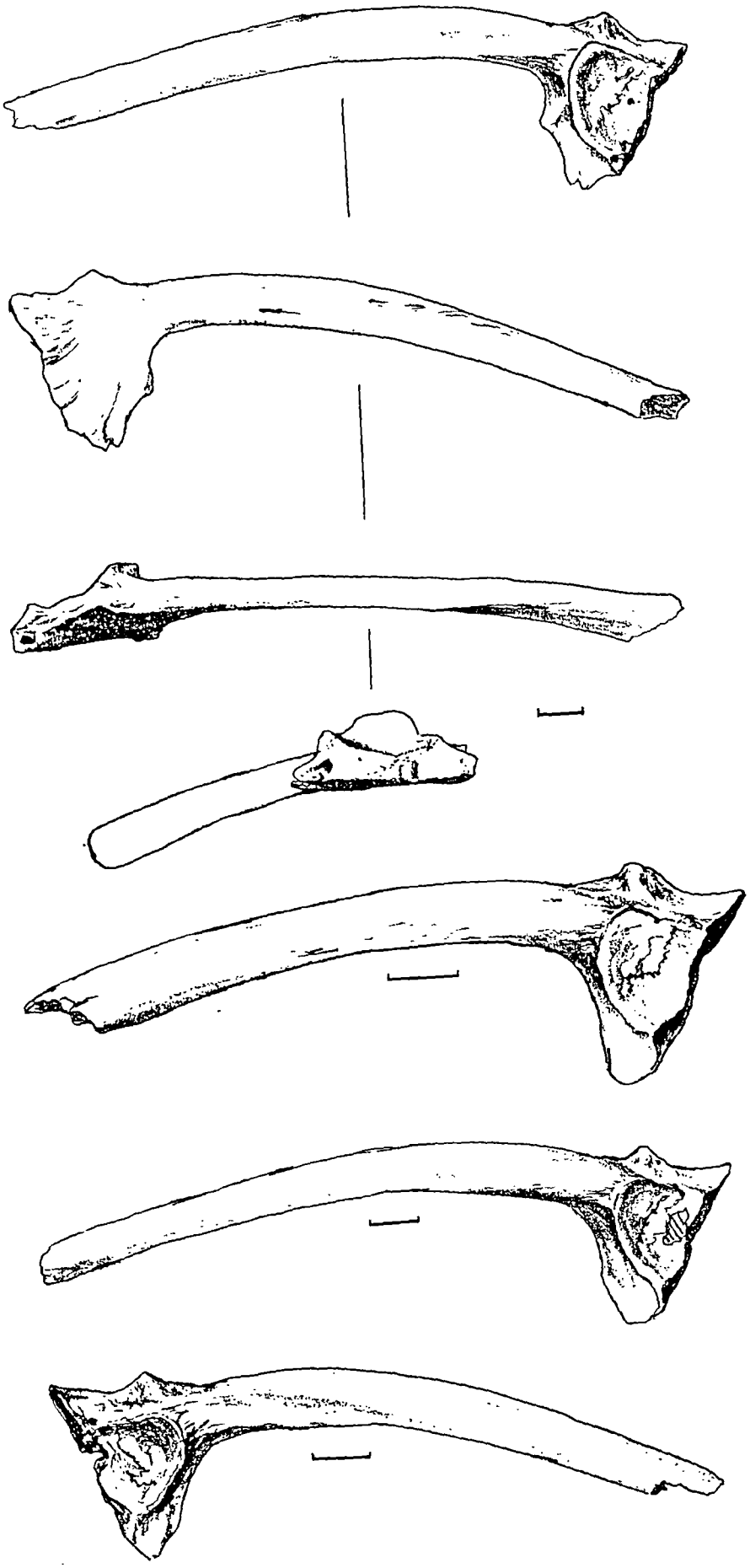


Figure 6.10: *B. calamita* ilia from Ightham fissure, Kent (BMNH: R10176).

CHISLET, KENT

Middle Pleistocene interglacial deposits are exposed in a section of a 19th Century gravel pit at Chislet Court, north Kent (NGR TR224650). The pit is now disused and overgrown. Topographically, the site is a terrace of the River Stour, with the land surface at around 8.5m OD. The area is not mapped well and exactly which terrace is represented is not known (D.H. Keen, pers. comm., 1998). Prestwich (1855) described a 5m high section exposed in gravels apparently close to this locality, and drew a comparison with the deposits at Clacton, Essex. The sequence comprised an upper layer of gravel and brick-earth around 1.0-2.5m thick, beneath this a 2.5-4.0m sequence of quartzose sand with clay laminations and plant matter, and chalk at the base. He noted the presence of a few undeterminate large mammal bones, marine and freshwater molluscs, Foraminifera and plant remains. Recent investigations and sampling (1996 and 1997) have been carried out by D.R. Bridgland, D.H. Keen and D. Schreve. The stratigraphy of a 4m section (Bridgland, pers. comm. to Keen, 1997) is as follows:

Unit 6	0.00-0.75/85m	Made ground
Unit 5	0.85-1.35m	Pale brown calcareous silt with race nodules (Sample 1)
Unit 4	1.35-1.65m	Dark yellow brown coarse to very coarse sand with shells and sub-angular flint pebbles (Sample 2)
Unit 3	1.65-2.65m	Dark yellowish brown sandy gravel with sub-rounded flint
Unit 2	2.65-2.90m	Olive-yellow pebbly silty fine sand with chalk and shell fragments
Unit 1	2.90-4.10m	Strong brown coarse loamy sub-angular flint gravel with some rounded Tertiary pebbles; gravel more compact than above; some race nodules, shells fragments; very large tabular flints at base (Sample 3 from sandy lens at 2.90-3.20m)

(Chalk rubble bedrock at 4.10m)

Molluscan analyses have yielded a temperate assemblage from Sample 2 (Unit 4), with the presence of woodland indicated by *Discus rotundatus* and numerous clausiliids (Keen, pers. comm., 1998). Freshwater species include two valves of the thermophile *C. fluminalis*, *Pisidium moitessierianum, P. amnicum* and the extinct *P. clessini.* Sample 1 (Unit 5) presents an altogether different assemblage, dominated by the cold-tolerant dry land species *Pupilla muscorum* which suggests the onset of climatic deterioration (Keen, pers. comm., 1998). Unit 4 also contained a few 'pebbles' of indeterminate large mammal bone (Keen, pers. comm.). Only preliminary small mammal studies have been carried out, but D. Schreve has identified Russian Desman (*Desmana moschata*) from Unit 4. The age of the interglacial layer at Chislet is uncertain. According to Schreve (pers. comm., 1997), the presence of *D. moschata* demands a Stage 9 age at the youngest. In altitudinal terms, the interglacial Unit 4 is no more than c.7m OD. Such a low elevation ought to preclude any age older than Stage 9, and perhaps even Stage 7. Preece (1995) noted that *P. clessini*

is known from Swanscombe, Clacton, Purfleet and Ilford (though not from Aveley), but is unknown from Last Interglacial or younger sites. Thus a Stage 7 or 9 age is probable for Chislet. Moreover, D.Q. Bowen (pers. comm. to Keen, 1997) has obtained 'Stage 7' amino acid ratios on *Valvata piscinalis* from Unit 4.

A few frog bones were among those picked by Keen from Sample 2 of the sand of Unit 4. The taxonomy of these bones is as follows: *R. temporaria/arvalis, Rana* sp. (brown frog), Anura indet. These few remains are currently in the possession of D. Schreve (NHM).

Systematic palaeontology

Rana temporaria/arvalis

Material. Sample 2. One partial left male second digit metcarpal.

Remarks. The metacarpal has large, roughened nuptial tubers, larger than in *R. dalmatina*.

Rana sp. indet. (brown frog)

Material. Sample 2. Two partial urostyles (one juvenile).

Remarks. These have the lateral edges of their ventral surface more acutely angled than in *B. bufo* with which confusion is possible. The posterior end of the neural spine is angled vertically rather than sloping cf. green frogs.

Indeterminate Anura

Material. Sample 2. One partial sacrum, one partial ischium, one partial left angulosplenial, one partial left and one partial right humerus (both juveniles), two phalanges and one metacarpal.

Remarks. These elements could all be *Rana*, but cannot be referred with certainty. The sacrum has only its centrum intact, with two elliptical condyles and the base of one diapophysis.

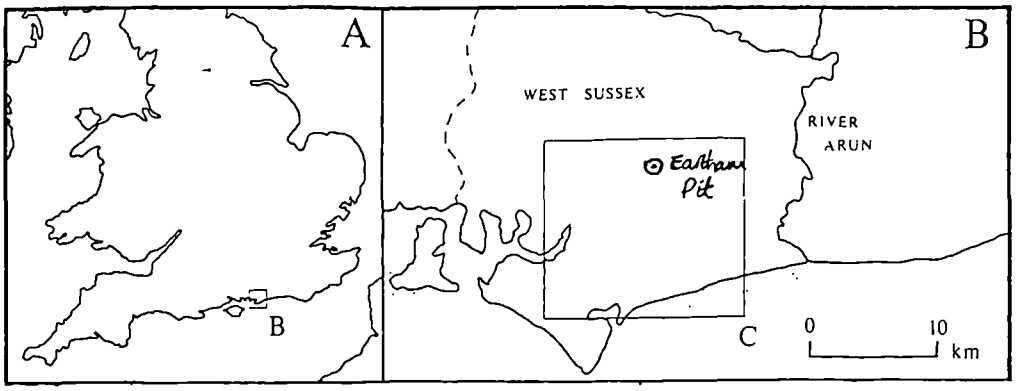
BOXGROVE, WEST SUSSEX

This site is within the Eartham Pit quarry operated by Amey Roadstone Company (NGR SU920085). It is situated at the northernmost edge of the Upper Coastal Plain where it abuts the truncated dip slope of the South Downs. Preliminary multidisciplinary findings were presented by Roberts *et al* (1986). The deposits begin with a series of marine sediments at the base of the sequence (the Slindon Sands), representing a relative sea-level rise of 42m. These were deposited as a beach under decreasingly intertidal conditions and grade into terrestrial and fluvial units higher up, with contemporary cliff collapse eventually denoting a transition to full periglacial conditions. Archaeological remains associated with a Unit 4c of the terrestrial Upper Slindon Sands include large amounts of debitage which has been successfully refitted. Two flint scatters are clearly arranged around the sitting position of a human (Roberts *et al*, 1986). Pollen analyses showed a dominance of arboreal taxa with pine, spruce, fir and lesser amounts of oak and beech (Scaife in Roberts *et al*, 1986). In the Upper Slindon Sands, pine constitutes over 80% of the pollen spectra and there are Hoxnian affinities. Small mammals include the evolved form of water vole, *Arvicola cantiana*, indicating a post-Cromerian (*sensu* West Runton Freshwater Bed) age (Currant in Roberts *et al*, 1986). Holman (1992a) identified the following herpetofaunal list from Boxgrove: *T. helveticus, T. helveticus/vulgaris, Triturus* sp., *P. fuscus, B. bufo, B. calamita, Bufo* sp., *R. arvalis, R. temporaria, Rana* sp., *A. fragilis, Lacerta* cf. *L. vivipara, N. natrix* and *Natrix* sp. Most of the remains came from Unit 4c (terrestrial phase, Upper Slindon Sands), but fewer remains came from throughout Units 4a and 4b (regression phase, Upper Slindon Sands), Units 5 and 6 (Fe/Mn layer, White/Grey Clay and Lower Brickearth). Stringer *et al* (1996) suggested correlation of Boxgrove Unit 4c with Westbury Cave Units 11-15 on biostratigraphic grounds.

During the current project, it was felt necessary to re-examine some of the herpetofaunal remains from Boxgrove, as identified by Holman (1992a). In particular, attention was drawn by the illustration of a '*T. vulgaris*' trunk vertebra given by Holman, which resembled *T. alpestris*. Though the criteria he used for diagnosis of newt vertebrae are useful, Holman did not consider any non-British species in his identifications of *Triturus*, and apparently allocated the remains to the most appropriate of the three native species. This is inconsistent with his treatment of other genera from the site. Pleistocene interglacial faunas, characteristically rather than exceptionally, include exotic species. Holman detailed thirty-five vertebrae, but only specifically identified one. He concluded that it did not belong to *T. cristatus*, identifying it as *T. vulgaris*. Also, for the same reasons that *B. calamita* identifications from Whitemoor Channel, Ightham Fissure and Cow Cave were re-examined, the *Bufo* ilia from Boxgrove ought to be checked.

The material is currently held at the NHM and S. Parfitt kindly allowed it to be studied. Sample numbers given below refer to the field excavation sample numbers, cf. Holman (1992a), but with some corrections made by S. Parfitt when labelling the individual boxes of bones for archiving. Re-examination of the material has led to a number of significant changes to Holman's (1992a) identifications. Five taxa (*T. vulgaris, T. vulgaris/helvetica, L.* cf. *vivipara, N. natrix* and

a)



b)

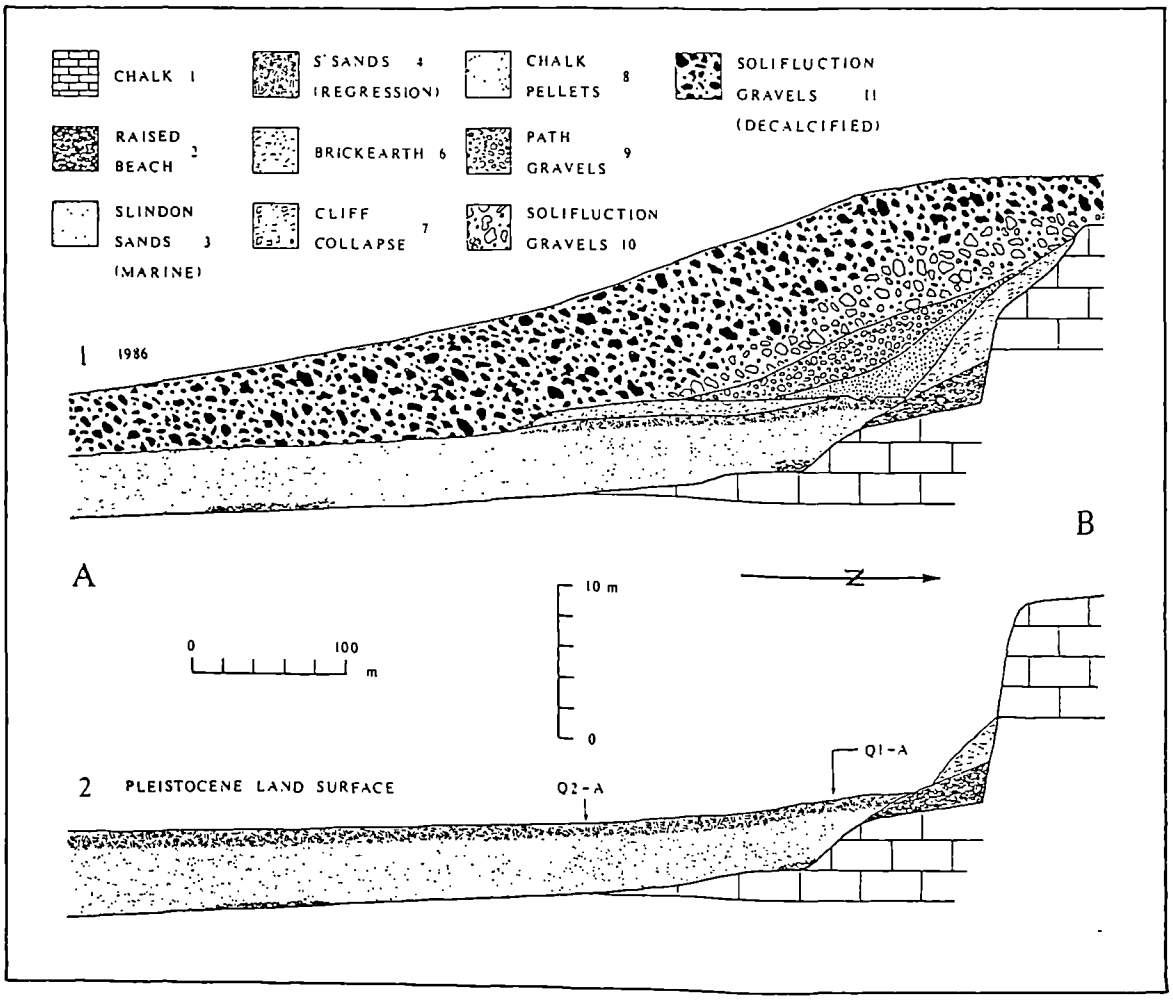


Figure 6.11: Boxgrove, West Sussex: a) Location; b) Lithostratigraphic section (after Roberts *et al*, 1986).

Natrix sp.) should be removed from the herpetofaunal list, and four others (*P. fuscus, B. calamita, B. bufo* and *R. arvalis*) require minor or major modifications. Seven additional taxa (*T. alpestris, T.* cf. *alpestris, Triturus* sp., Anura indet., cf. *Vipera* sp., *N. maura/tessellata* or *V. berus,* and Ophidia indet.) should be added to the herpetofaunal list. It is thus advised that the revised herpetofaunal list from Boxgrove should be as follows: *T. alpestris, T.* cf. *alpestris, Triturus* sp., *P.* cf. *fuscus, B. bufo, B.* cf. *bufo, B. calamita, B.* cf. *calamita, R. temporaria, R.* cf. *arvalis, Rana* sp., Anura indet., *A. fragilis,* cf. *Vipera* sp., *N. maura/tessellata* or *V. berus*, Ophidia indet. The descriptions and modifications are presented below.

Systematic palaeontology

Triturus alpestris

Material. #88-701 (Unit 4b). One trunk vertebra.

Remarks. This vertebra was identified as '*T. vulgaris*' by Holman (1992a). As suspected from the drawing given by Holman (see Figure 3.4a), it is in fact *T. alpestris*. The vertebra is too elongate to be *T. vulgaris* or *T. helveticus*. Its zygapophyses are also too produced. The ventral laminae are fairly narrow and robust, and could be described as intermediate between *T. vulgaris* and *T. cristatus*. The neural spine is robust, and in lateral view it slopes upwards slightly towards the posterior neural arch. The posterior neural arch is deeply indented, and in posterior view it is quite rounded, with a semicircular profile. Its lateral walls are thick, each with a bulbous nodule on their internal facets, somewhat resembling the zygantrum in snake vertebrae. The bone is quite constricted behind the transverse processes, ahead of the postzygapophyses. The anterior condyle is noticeably produced. The label associated with the bone had already been altered from '*T. helveticus*' to '*T. vulgaris*' by Holman, perhaps indicating uncertainty over the identification. However, it does not appear that Holman (1992a) considered *T. alpestris* as a possibility in his identification.

Triturus cf. *alpestris*

Material. #87-251 (Unit 4c). One partial trunk vertebra.

Remarks. This is the most complete specimen out of seven vertebrae refered by Holman (1992a) to '*T. vulgaris* or *helveticus*'. It consists of much of the centrum (except the posterior cotyle), the right side including part of the neural wall and the right prezygapophysis. The posterior end of the right neural wall is sculpted with oblique ribs and cusps. The right prezygapophysis protrudes markedly, and the overall morphology in right profile is cf. *T. alpestris*.

Triturus sp. indet.

Material. #87-251 (Unit 4c). Six partial and fragmentary vertebrae.

Remarks. These were identified as '*T. vulgaris* or *helveticus* by Holman (1992a). All are in poor condition, variously eroded and incomplete. They should all be referred to *Triturus* sp. and

certainly cannot be identified as *T. vulgaris* or *T. helveticus*.

Pelobates cf. *fuscus*

Material. #86-8 (Unit 4c). One left ilium. #88-910 (Unit 4c). One juvenile left ilium. #88-461 (Unit 4c). One right ilium.

Remarks. These ilia were probably correctly identified by Holman (1992a) as '*P. fuscus*', but a slight amount of uncertainty should be acknowledged owing to the similarity of *P. fuscus* and *P. cultripes* ilia. Nevertherless, the apparent syntopic occurrence of *R. arvalis* evidenced from the same unit certainly points towards *P. fuscus* rather than *P. cultripes*. #86-8 (Unit 4c). This ilium has its pars descendens missing, thus removing one possible identification criterion for separation from *P. cultripes*. The pars ascendens is convex and there is a deep transverse dorsal notch at the junction of the ala and the corpus, typical of *Pelobates*. The truncated ala is incomplete, but has a very flattened lateral face cf. *P. fuscus*. There are two foramina on the ala, beneath the angle of the ventrolateral ridge. #88-910 (Unit 4c). This specimen has much of the corpus missing. The pronounced dorsal notch is deep and wide in dorsal view, and identifies it as *Pelobates*. The anterior acetabular wall is indented at its base. The ala is robust with a flattened lateral face and two parallel foramina just above and below the ventrolateral ridge. The pars ascendens is convex, slightly undulating to form a low tuber superior, and has its tip missing. #88-461 (Unit 4c). The pars descendens and lower part of the corpus are missing. The pars ascendens is intact and slightly convex, with a low undulating tuber (similar to *Bombina*). The dorsal notch is obvious and has black and white crystals attached to it. The ala is slightly bulbous near its junction with the corpus, on the lateral side of the dorsal notch. The lateral face of the ala is fairly flat, with one foramen. The ala has previously been glued to repair breakage.

Bufo bufo

Material. #87-100 (Unit 4c). One partial left ilium (immature). #87-36 (Unit 4c). One left ilium. #87-181 (Unit 4c). One right ilium. #87-97 (Unit 4c). One left ilium. #87-114 (Unit 4c). One right ilium.

Remarks. According to their diagnostic features, all five of these ilia were correctly identified by Holman (1992a). #87-100 (Unit 4c). The tuber is bulbous but pinched in a way typical of *B. bufo*. #87-36 (Unit 4c). This ilium was figured by Holman (1992a). Its tuber is rounded, bulbous and 'pinched'. The ala is broken but not distinctly flattened into a ridge or blade. #87-181 (Unit 4c). The tuber is low, with two bulbous areas. The pars descendens is missing, but appears to have been twisted medially thus creating a concave medial face. #87-97 (Unit 4c). This specimen is almost complete (15mm long, adult). #87-114 (Unit 4c). The tuber is low but of typical *B. bufo* form.

Bufo cf. *bufo*

Material. #87-251 (Unit 4c). One right ilium.

Remarks. #87-251 (Unit 4c). This ilium was identified as '*B. bufo*' by Holman (1992a), alongside a left ilium which is referred to *B.* cf. *calamita* below. The tuber of this specimen is rounded and fairly typical of *B. bufo*, but a referral to *B.* cf. *bufo* would probably be most suitable.

Bufo calamita

Material. #86-75 (Unit 6a). One left ilium. #87-72 (Unit 5a). One left ilium.

Remarks. #86-75 (Unit 6a). This ilium was identified as '*P. fuscus*' by Holman (1992a). It has a low, triangular, flat-sided, pyramidal tuber. The ala has a very flat lateral side, cf. the typical 'blade' of *B. calamita*. The pars descendens is narrow and partly missing. There is no dorsal notch cf. *Pelobates*, and this specimen quite clearly belongs to *B. calamita*. #87-72 (Unit 5a). This ilium was correctly identified by Holman (1992a) as *B. calamita*. It has a somewhat laterally bulbous tuber, but with an anterolateral groove cf. a Spanish specimen seen (MNCN #15455). The ala is truncated but has a very deep groove and a correspondingly strong ventrolateral blade. The pars descendens is narrow and broken.

Bufo cf. *calamita*

Material. #88-522 (Unit 4c). One left ilium. #87-251 (Unit 4c). One left ilium.

Remarks. #88-522 (Unit 4c). This specimen was identified as '*B. bufo*' by Holman (1992a), but it is quite likely to be *B. calamita*. The tuber is roughened and laterally bulbous but is within the morphological range of Spanish specimens (MNCN #15455, #15456, #15469). The angle of attachment of the ala to the corpus is very obtuse (c.180°). The ala is truncated but is apparently flattened into a blade. The ilium is in a box (labelled '*B. bufo*') with a partial sacrum and a female right humerus. #87-251 (Unit 4c). This was identified by Holman (1992a) as '*B. bufo*' and placed in a box alongside another ilium which is referred above to *B.* cf. *bufo*. It has a very elongate, blade-like tuber. This is similar to a Spanish specimen seen, but the dorsal edge is sharper, longer and not as dorsally prominent. The ala is truncated but appears compressed into a ventrolateral ridge/blade.

Rana cf. *arvalis*

Material. #87-251 (Unit 4c). One partial left ilium.

Remarks. #87-251 (Unit 4c). This specimen was identified and figured as '*R. arvalis*' by Holman (1992a), but it would be preferred here if *R.* cf. *arvalis* was used. The corpus is largely absent. The ala is also truncated, but the tuber and vexillum are intact. The gracile tuber has a tapered and neatly faceted form, cf. the Swedish juvenile (C. Snell collection). Perhaps such subtle forms as this would support the use (e.g. cf. Holman *et al*, 1988) of separate subspecies *R. a.*

wolterstorfii and *R. a. arvalis* as illustrated by Böhme (1977). The Boxgrove specimen would appear to be of the *R. a. arvalis* form as its tuber is neatly faceted and less well developed. Taken alone, this specimen might be difficult to separate from *R. temporaria*. However, the Boxgrove *R. temporaria* are clearly distinct from it, with low, ribbed tubers and depressed vexillums (see Holman's figures reproduced in Figure 3.4e,f).

Indeterminate Anura

Material. #87-251 (Unit 4c). One partial right angulosplenial.

Remarks. Remarkably, this bone was identified as a "tiny jaw fragment" of *Natrix* sp. by Holman (1992a). It is not a snake bone, but belongs to an anuran. The anterior end is missing. The posterior portion is very thick and the sulcus is particularly narrow beneath the coronoid process. It does not appear to belong to *Bufo* or *Rana*, and could conceivably belong to *Pelobates*. Unfortunately, *Pelobates* angulosplenials have not been studied and identification is therefore not possible.

Anguis fragilis

Material. #87-156 (Unit 4c). One caudal vertebra.

Remarks. This incomplete specimen was recorded as a trunk vertebra of '*L.* cf. *vivipara*' by Holman (1992a). It is, in fact, a small but recogniseable *A. fragilis* caudal vertebra. The transverse processes and ventral process are truncated, but there is a clear suture towards the anterior end. This is obviously not present in *L. vivipara* trunk vertebrae.

cf. *Vipera* sp. indet.

Material. #86-36 (Unit 4c). One juvenile trunk vertebra. #87-123 (Unit unknown). One trunk vertebra.

Remarks. #86-36 (Unit 4c). This incomplete specimen is labelled '*Natrix* sp.', but was referred to '*N. natrix*' by Holman (1992a). It is also the specimen illustrated by Holman (shown here in Figure 3.4i), despite his illustration being labelled '*Natrix natrix* (86-68, 5a)'! The vertebra is from a juvenile, and as its posterior neural arch is quite low with straight-sloping rather than convex sides, it is unlikely to belong to *Natrix*. Its broken hypapophysis precludes specific identification. #87-123. This specimen is labelled '*Natrix* sp.' but was not described by Holman (1992a).

Natrix maura/tessellata or *Vipera berus*

Material. #86-2 (Unit 4c). One fragmentary vertebra. #86-68 (Unit 5a). One fragmentary vertebra. #? (No code). One fragmentary vertebra.

Remarks. #86-2 (Unit 4c). Remarkably, this fragment was identified as '*N. natrix*' by Holman (1992a), despite the fact that it consists of only an isolated hypapophysis. This is acutely

pointed and certainly does not belong to *N. natrix*. This form of hypapohysis is found in *N. maura, N. tessellata* and *V. berus*. #86-68 (Unit 5a). This fragment was identified as '*N. natrix*' by Holman (1992a), along with two fragments referred to Ophidia indet. below. It consists only of the posterior condyle with a complete and acute hypapophysis. #? (No code). This specimen is in a small vial labelled '*Natrix* sp.', but has no sample code. It is a posterior condyle with most of the hypapophysis intact. The acute form of the hypapophysis allows the identification suggested here. Because the juvenile vertebra described above is cf. *Vipera* sp. rather than *Natrix* sp., it is very likely that these fragments are in fact *V. berus* rather than *N. maura/tessellata*. However, though the material can be treated informally as *V. berus*, an element of uncertainty must be acknowledged in the formal identification.

These fragments form only a tiny part of the snake vertebra. None are complete enough to infer that they are trunk rather than cervical vertebrae. Certainly none is identifiable as *N. natrix* as reported by Holman (1992a).

Indeterminate Ophidia

Material. #86-68 (Unit 5a). Two fragmentary vertebrae. #87-251 (Unit ?). One fragmentary vertebra.

Remarks. #86-68 (Unit 5a). These were identified as '*N. natrix*' by Holman (1992a). Each fragment consists of only the posterior condyle, with the hypapohysis and the rest of the vertebra missing. There is no way of identifying them further. #87-251 (Unit ?). This fragment was identified as '*Natrix* sp.' by Holman (1992a). It consists of only the posterior condyle with an incomplete hypapophysis. It cannot be identified to genus.

6.2 Southwest England

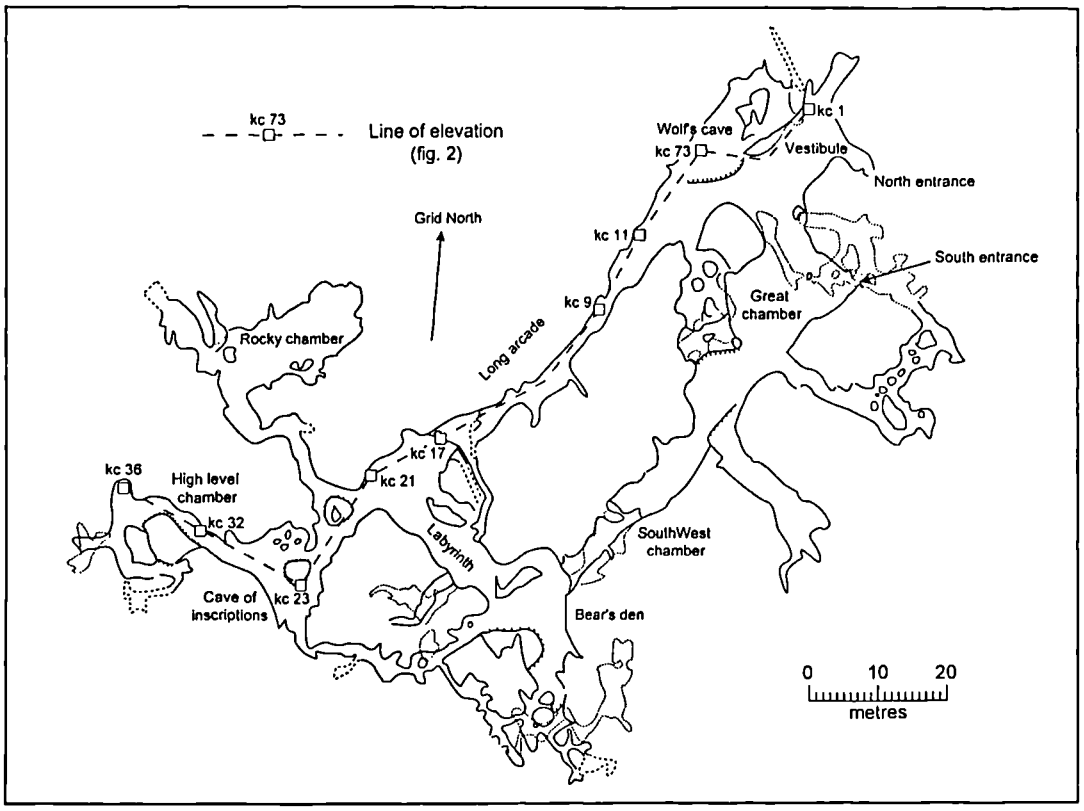
KENT'S CAVERN (WOLF DEN), TORQUAY, DEVON

Kent's Cavern (NGR SX934641) is an extensive cave system, located in Wellswood, 2km east of Torquay town centre. It has a long history of 19th Century excavations by McEnery, Pengelly and the Torquay Natural History Society. The sedimentary record spans from the Middle Pleistocene to the Holocene, though there is apparently a large hiatus between what may be Stage 9 or Stage 11 deposits and the Devensian sequence (Proctor, 1996). Most of the cave was excavated to a depth of between 1.2m and 2.4m by Pengelly between 1865 and 1880 (Proctor, 1996). However, recent investigations have shown that intact seqences still exist and that these have been important in elucidating the overall stratigraphy of Kent's Cavern (Proctor, 1996). Figure 6.12 shows a schematic representation of the sediments and a survey of the cave.

The lowest sedimentary unit is the Breccia, which consists of a chaotic conglomerate of debris-flowed cobbles and gravel in a dense clayey matrix (Proctor, 1996). The limited faunal finds are dominated by cave bear (*Ursus deningeri*), and Acheulian implements are also present. Uranium series (U-Th) and electron spin resonance (ESR) dating of speleothem associated with the breccia indicates an age between 3-400ka BP, which Proctor (1996) correlated with marine Stages 9 and 11. Overlying the Breccia is a thick, massive layer of speleothem, the Crystalline Stalagmite, probably deposited while the cave was sealed from outside inputs of sediment. A thick sequence of Cave Earth overlies this, and can be divided into three parts. The Wash Facies at the base is a poorly sorted mixture of cobbles and finer sediments, resulting from erosion of underlying sediments by a stream which probably also opened up the cave entrance (Proctor, 1996). The subsequent Loam/Stony Cave Earth is a silty clay with angular limestone deposited by a combination of processes, and entering the cave via the entrance. It contains a diverse and abundant Devensian cold-stage fauna, with spotted hyaena, mammoth and woolly rhinoceros, and is interpreted as a hyaena den (A.P. Currant, pers. comm. to Proctor). A sequence of Middle and Upper Palaeolithic industries culminates in a Late Upper Palaeolithic hearth deposit, the Black Band. A bovid vertebra from the Black Band yielded a radiocarbon date of 11,570±410 ^{14}C BP (BM-2168) (Jacobi *et al*, 1986). According to Proctor (1996), a soft, porous Granular Stalagmite layer overlying the Cave Earth must therefore be Holocene, though no more specific age estimate was possible.

An area known as the Wolf's Cave or Wolf Den was excavated in 1995, and the findings of the multidisciplinary team have yet to be published. A bedded sequence of cave earth in the Wolf Den apparently spans much of the last 40,000 years (Proctor, pers. comm. to C. Price, 1996). A spit was excavated and samples were taken at ten-centimetre intervals in vertical sequence. These yielded a small mammal fauna, some of which appears to be mixed in its climatic affinities (C. Price, pers. comm., 1997). A series of nine samples from the upper part of the sequence (A at the top, I at the bottom), have produced herpetofaunal remains. This part of the sequence corresponds

a)



b)

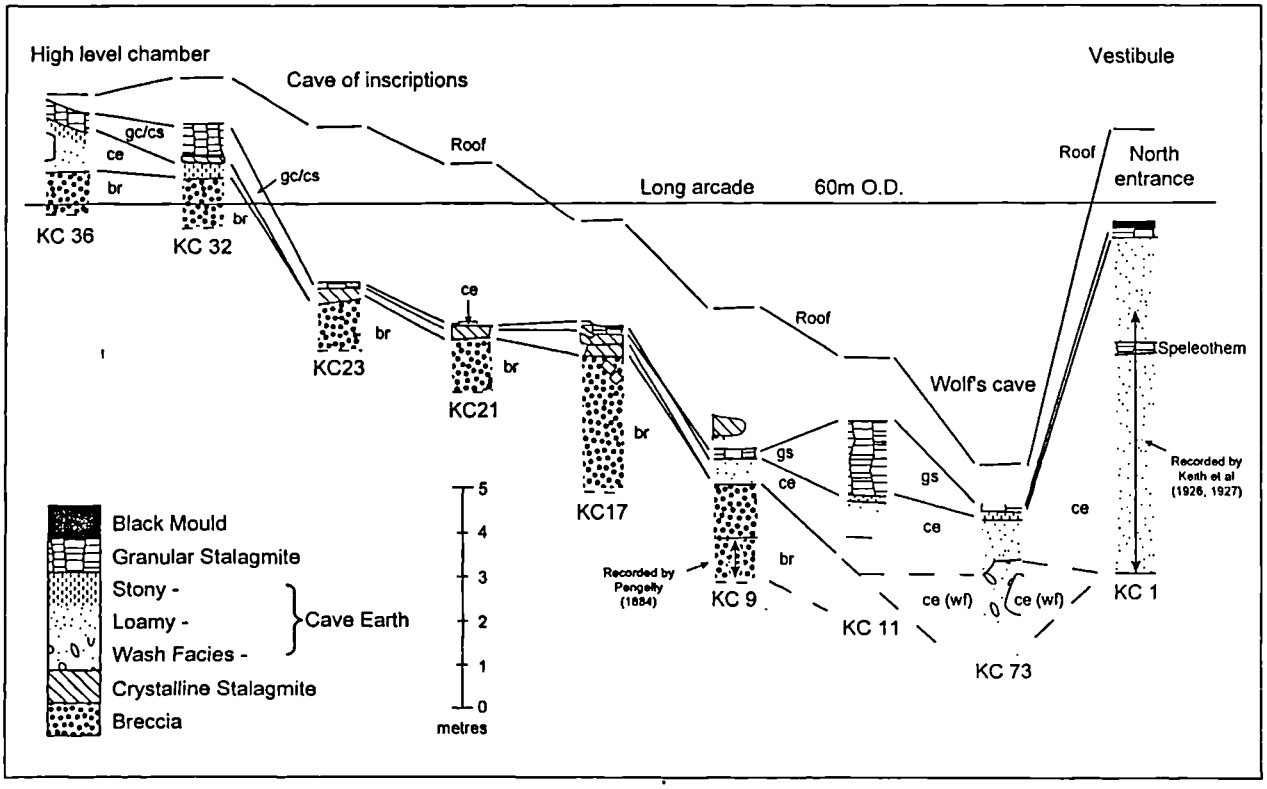


Figure 6.12: Kent's Cavern, Devon: a) Survey of the cave; b) Schematic relationships between the deposits (after Proctor, 1996).

with the Stony and Loamy Facies of Proctor (see Figure 6.12b), the top of which ought to date to the Lateglacial.

This site provided a rare opportunity to study a vertically continuous sequence of herpetofaunal remains, in stratified samples. The herpetofaunal remains are generally in good condition and, although some are partly crushed, most elements are surprisingly well preserved. A total of forty-one specifically identified bones are recorded, twenty-one of these (representing five species) were from layer F. The following composite herpetofaunal assemblage was identified: *B. bufo, B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, V. berus.* Table 6.2 shows the taxa recovered from each sample. The material is currently in the author's possession but will be housed at the NHM in due course.

It was suspected that the presence of *B. calamita* in sample F might support the supposed age for the upper part of the Cave Earth, and correspond with the Lateglacial Interstadial, hence a sample was submitted for AMS dating. The determination on a single trunk vertebra in fact yielded an early Holocene age of 9,690±140 ^{14}C BP (OxA-6979) which was calibrated using CALIB 3.0 (Stuiver and Reimer, 1993) to 10,945 cal BP. Evidently, the top of the Cave Earth in the Wolf's Den must be younger than had previously been imagined. The lack of thermophiles from sample G could correspond with the Lateglacial Stadial (Younger Dryas), in which case sample H, which contains a thermophile (*Bufo* sp.), could be of Lateglacial Interstadial age. Furthermore, if sample F is early Holocene, then the overlying sequence of 60cm ought to be younger than this. However, the problem of apparent mixing (Price, pers. comm., 1996) must be addressed, and further ^{14}C-dating would be advantageous. Also, the age of the overlying speleothem should be considered with respect to other such deposits in caves of the southwest. For example, a surficial speleothem layer in Lower Cave, Bristol (see below) was U-Th dated to between 5-7ka BP (A. Baker, pers. comm., 1998). If mixing of the Wolf Den sediments has not been wholesale, then a radiocarbon age of c.7ka BP could perhaps be expected for sample A. A very similar age was obtained on *B. calamita* from Cow Cave (discussed below).

Table 6.2

Depth (cm)	Sample	Species	Total number of specifically-identifiable elements
0-10	KC 73 A	*R. temporaria,* Anura indet.	2
10-20	KC 73 B	*R. temporaria,* Anura indet., *V. berus*	2
20-30	KC 73 C	*R. temporaria,* Anura indet., *V.berus*	3
30-40	KC 73 D	*R. temporaria,* Anura indet.,*V. berus*	6
40-50	KC 73 E	*Rana* sp., Anura indet., *V. berus*	6
50-60	KC 73 F	*B. bufo, B. calamita, Rana* sp., Anura indet., cf. *L. vivipara, V. berus*	21

60-70	KC 73 G	*Rana* sp., Anura indet., cf. *L. vivipara*	1
70-80	KC 73 H	*Bufo* sp., *R. temporaria,* Anura indet.	1
80-90	KC 73 I	*Rana* sp., Anura indet.	0

Systematic palaeontology

Bufo bufo

Material. KC73 F. Two left ilia.

Remarks. Tubers are well-rounded and relatively diminutive, pars descendens narrow and unangled.

Bufo calamita

Material. KC73 F. One sacrum, one right ilium, four trunk vertebrae and two radioulnae.

Remarks. The sacrum has very widely flared lateral apophyses and a V-shaped dorsal ridge. Unusually, it has only one posterior articulation (cf. *Bombina*), with an elongate outline. The ilium has much of the corpus missing, but the anterior part of the tuber is intact, showing its straight edge and smooth, slightly concave slope. The trunk vertebrae are compact, with close-set zygapophyses. The diapophyses slope upwards, and are positioned high, in line with the neural arch roof. The radioulnae are robust and wide at their distal end, their radii have a sinuous outline, and the olecranons are well rounded. One trunk vertebra was submitted for AMS radiocarbon dating (OxA-6979).

Bufo sp. indet.

Material. KC73 F. One trunk vertebra, two right humeri, three radioulnae, three femora, two tibiofibulae, one coracoid, one tibiale, two fibulare and one male II metacarpal. KC73 H. One tibiofibula.

Rana temporaria

Material. KC73 A. One right ilium and one male left humerus. KC73 B. One left ilium. KC73 C. One left ilium. KC73 D. One left ilium. KC73 H. One left illium.

Remarks. The ilium from sample A has a relatively low, shallow-sloping tuber which descends steeply on its posterior side to a very low medially-deflected vexillum. The other ilia of the typical subfossil form, with ribbed tubers and vexillums sloping down and medially. The ilium from sample H has a strong and deeply-incised tuber, with a strong (though incomplete) vexillum.

Rana sp. indet. (brown frog)

Material. KC73 A. One right scapula, one femur and one tibiofibula fragment. KC73 B. One partial radioulna, one partial femur and two partial tibiofibulae. KC73 C. One partial scapula,

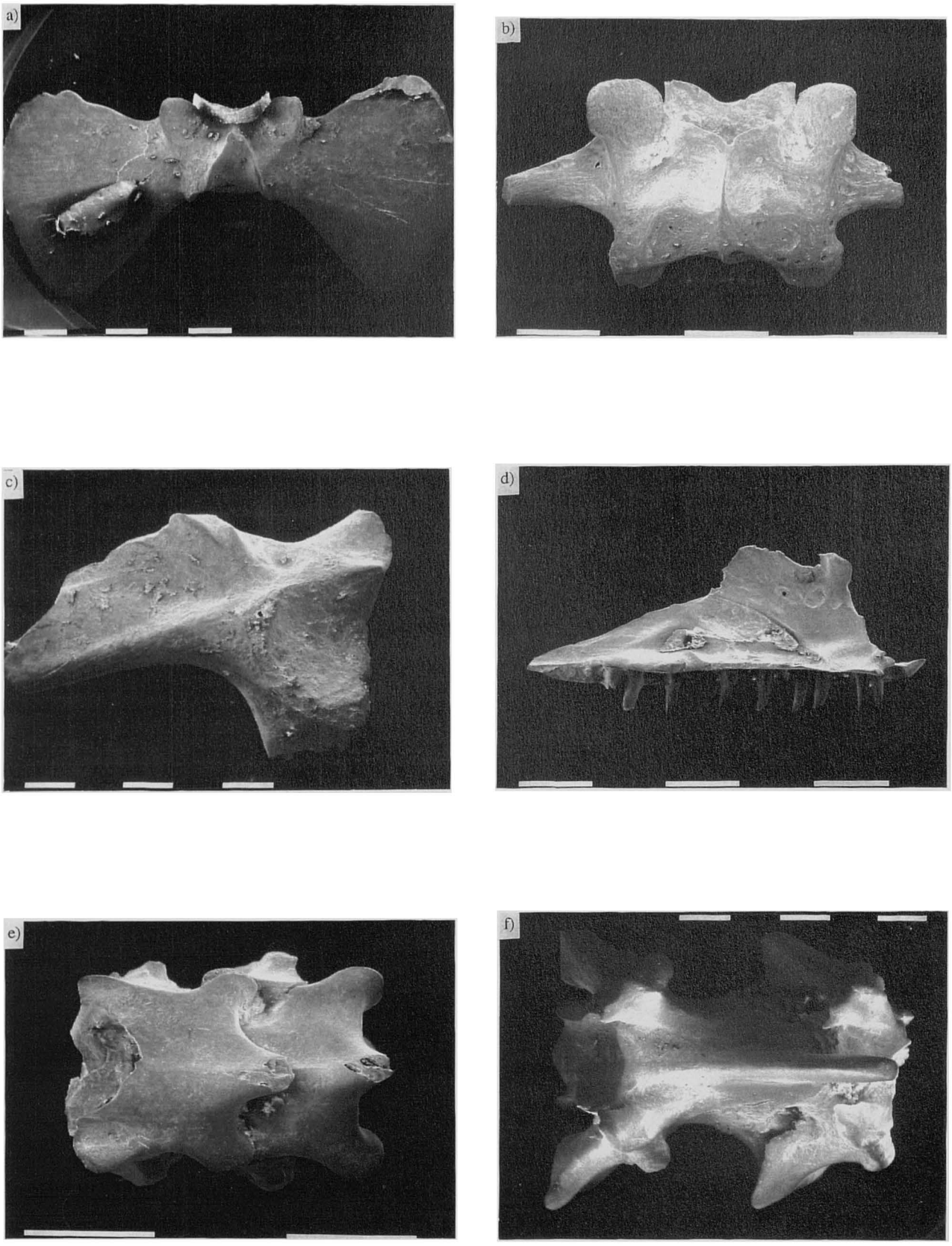


Figure 6.13 Herpetofaunal remains from Wolf's Den, Kent's Cavern: sacrum (dorsal view) of *B. calamita* (sample KC 73F); b) trunk vertebra (dorsal view) of *B. calamita* (sample KC 73F); c) left ilium (lateral view) of *R. temporaria* (sample KC 73H); d) left maxilla (medial view) of cf. *L. vivipara* (sample KC 73F); e) associated trunk vertebrae (Dorsal view) of cf. *L. vivipara* (sample KC 73F); f) pathological fused trunk vertebrae of *V. berus* (sample KC 73E).

one right maxilla and one maxillary fragment, two partial tibiofibulae and one left angulosplenial. KC73 D. One left and one right maxilla (partial), one tibiofibula, one vertebra and one sacrum. KC73 F. One sacrum, one right angulosplenial, three tibiofibulae and one coracoid. KC73 G. One radioulna, one sacrum and one tibiofibula. KC73 I. One partial right ilium.

Remarks. This material is easily separated from *Bufo*, and can be distinguished on the whole from green frog *Rana*. It is likely that it also belongs to *R. temporaria*, but these elements are not sufficiently diagnostic for specific determination.

Indeterminate Anura

Material. KC73 A. One vertebral fragment, one partial urostyle and one phalanx. KC73 B. Two metacarpals. KC73 C. Two humeri, ten metacarpals and phalanges. KC73 D. One partial radioulna, one tibiale and three phalanges. KC73 E. One humerus and one phalanx. KC73 F. One partial sacrum, two left humeri, one quadratojugal, three vertebral fragments, one urostyle and twenty appendicular elements and fragments. KC73 G. One partial humerus and one limb fragment. KC73 H. One vertebral fragment and one limb fragment. KC73 I. One partial urostyle.

cf. *Lacerta vivipara*

Material. KC73 F. One left dentary, one left maxilla, four trunk vertebrae (two associated), one postsacral vertebra and one anterior half of a postsacral vertebra. KC73 G. One postsacral vertebra.

Vipera berus

Material. KC73 B. One trunk vertebra. KC73 C. Two trunk vertebrae. KC73 D. Five trunk vertebrae and four vertebral fragments. KC73 E. Two associated (possibly pathogenically fused) trunk vertebrae, four separate trunk vertebrae and a vertebral fragment. KC73 F. Three trunk vertebrae.

Remarks. The trunk vertebrae have low posterior neural arches and sloping zygapophyses. In examples where the hypapophysis is complete, it is acute and strongly posteriorly-directed, reaching beyond the condyle. The fragments include several hypapophyses of typical tapering and pointed viperid form. By comparison of the largest vertebrae with those of a recent specimen, it is estimated that they belonged to an animal of c.640mm total length. This is comparable to the usual maximum size of an adult *V. berus* (Arnold and Burton, 1978).

COW CAVE, CHUDLEIGH, DEVON

Cow Cave (NGR SX864787) is one of a number of small caves in the Chudleigh gorge of the River Teign and was excavated by J.W. Simmons in 1962-63 (Holman, 1988). There do not appear to be any published details on the excavations and stratigraphy.

Holman (1988) described herpetofaunal remains from these excavations, which he believed to be of Devensian Lateglacial and/or early Holocene age. His list is as follows: *B. bufo, B. calamita, R. temporaria, A. fragilis* and *V. berus*. According to Holman, the remains came from four layers which were excavated in the 'back section' of the cave. *B. bufo* was recorded from layers I, II and IV; *B. calamita* from layer IV; *R. temporaria* from layers I, II and IV; *A. fragilis* from layers II and IV; and *V. berus* from layers II and IV (Holman, 1988). It should be noted that R. Jacobi (pers. comm., 1997), who is familiar with the excavations and faunal material, is of the opinion that Holman misinterpreted the stratigraphic system used in Simmons' excavations.

Holman (1988) considered this fauna to represent a somewhat cooler period than that of Ightham (to which he attributed an Early Holocene age; Holman, 1985). There is arguably no evidence in the Cow Cave assemblage for a less temperate climate than at Ightham, other than the fauna being relatively impoverished. The absence of any herpetofaunal remains from Layer II could indicate a Younger Dryas age. Unfortunately, no sedimentological descriptions have been seen. Nevertheless, a radiocarbon determination carried out on a *B. calamita* ilium (from Layer IV) gave an age of 9,270±70 ^{14}C BP (OxA-6992). Using CALIB 3.0 (Stuiver and Reimer, 1993), this converts to a median calibrated date of 10,253 cal BP, and even at a two sigma deviation the oldest possible date is 10,439 cal BP. As Holman (1988) suspected mixing of the sediments at Cow Cave, it is not known whether any of the *B. calamita* remains are older than this. Nevertheless, an early Holocene age for *B. calamita* at Cow Cave fits with that from Kent's Cavern. Further dates from both sites would be useful, especially to ascertain whether any of the herpetofaunal remains are Lateglacial, cf. Broken Cavern.

The herpetofaunal remains from Cow Cave are held at the NHM. In the light of the current study, the *Bufo* material has recently been re-examined. The previous identifications (Holman, 1988) are supported for most of the *B. calamita* ilia, but some ilia have been re-assigned to *B. bufo*. Three boxes of ilia (NHM: R10197, R10183, R10188), labelled as *B. calamita*, were re-examined. Each ilium was considered, using the criteria described earlier. In cases where the previous identification was not correct, the ilia were re-accessioned in a separate box (currently without an accession number), labelled '*B. bufo*'. The herpetofaunal list given by Holman (1988) remains unchanged. A systematic account of the changes to identifications of individual elements is given below.

Systematic palaeontology

Bufo bufo

Material. NHM: (Awaiting new number). Five left and two right ilia, removed from NMH:

R10183 and R10188.

Remarks. Tubers are rounded, two are sub-cuboid, and laterally-protrusive. Three specimens have tubers fairly triangular, but lateral face on each is bulbous or rugose. Ridges on ala well-developed, sometimes with deep groove, but not blade-like. Ridge does not break ventral outline of ala. Pars descendens are relatively narrow, unangled, unremarkable. One with flanged connection with ala (see also '*Bufo* sp' below). Most are easily distinguished as *B. bufo*, without consideration of additional criteria described earlier.

Bufo calamita

Material. NHM: R10197. One left and one right ilium. NMH: R10183. Four left and two right ilia remaining. NHM: R10188. Five left and five right ilia remaining.

Remarks. State of presevation variable, some specimens have their ala largely missing. As the upper part of the corpus is the strongest part of ilium, the tubers are intact, even when the ala and pars descendens are partly or entirely missing. One specimen has clearly been rolled, but is still diagnostic. Tubers are generally sharply pointed, triangular and pyramidal. One has strong ridge to its peak, and a minor ridge radiating to the tuber's anterior slope. A depression is found between these, in the tuber's slope. One ilium has a bulbous area on the anterior flanks of the tuber, but is overall triangular and well-defined. Two ilia have less well-defined tubers, identification was aided by a strong ventrolateral blade and wide pars descendens. Ventrolateral blade not well developed in some cases, and not diagnostic. Pars descendens not consistent, some wide but unangled, others angled. Some with pars descendens relatively narrow, one with a strongly overlapping acetabular margin. Generally, identification relied upon an intact and well-defined tuber, but diagnosis was aided in some cases by other features. One of the ilia was submitted for AMS radiocarbon dating (OxA-6992).

Bufo sp. indet.

Material. NHM: (awaiting new number). One right ilium, length 10mm.

Remarks. Tuber fairly low, rounded, but not laterally protrusive. Peak not pointed, tuber not diagnostic. Ridge/groove not well-developed, does not break outline of ala. Pars descendens unusually wide around connection with ala, but narrow and unangled lower down. Probably immature specimen, cannot identify to species with certainty.

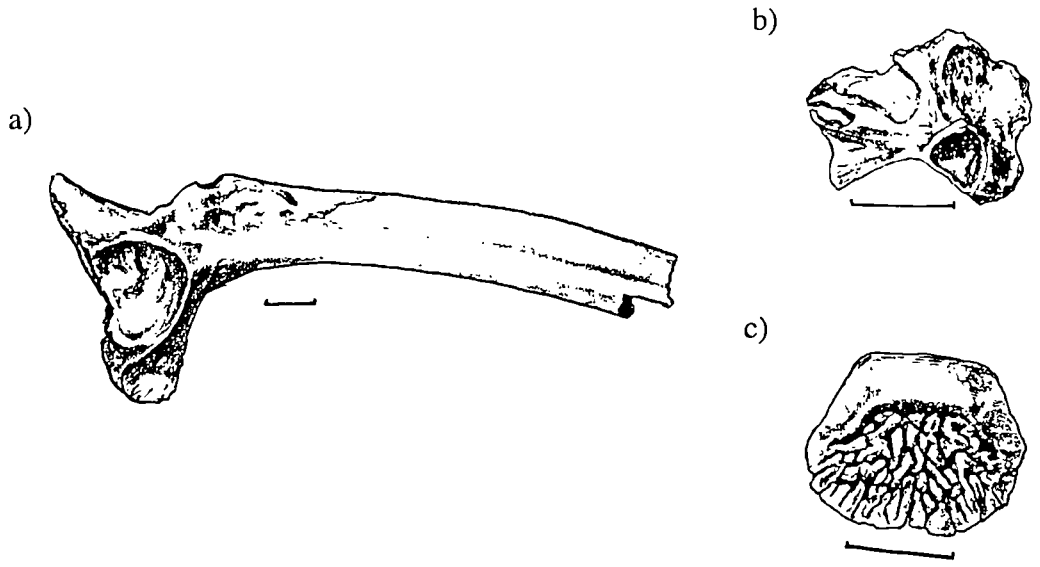


Figure 6. : Amphibian and reptile remains from Three Holes Cave (a-b) and Broken Cavern (c), Torbryan: a) right ilium of *R. temporaria* with toothmarks (THR146); b) left scapulocoracoid of *T. vulgaris/helveticus* (THR345); c) osteoderm f *A. fragilis* BRK409).

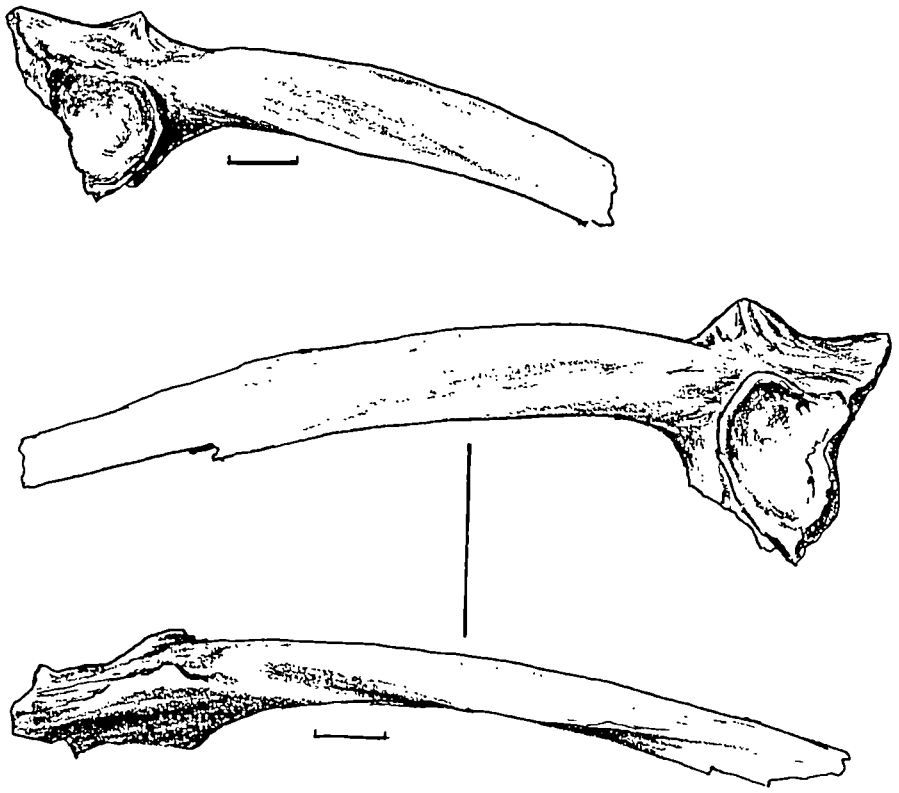


Figure 6.14: *B. calamita* ilia from Cow Cave, Devon (BMNH: R10183).

TORBRYAN CAVES, TORBRYAN, DEVON

Several caves in the Torbryan Valley (Figure 6.15a) have been excavated by the BM between 1989 and 1992. The Torbryan Valley is situated to the east of the Am Brook, a tributary of the River Dart. It is deeply incised into Devonian limestone and lies mid-way between the granite uplands of Dartmoor and the coast to the south. A full account will be given in due course (Roberts, in prep.), but a description of the recent work was given by Roberts (1996) and the authors therein. Together, the caves have produced vertebrate remains and archaeology from the Middle to Late Pleistocene and Holocene.

Herpetofaunal remains from three caves were studied during visits to the BM in 1995. These were extracted from tubes of small vertebrate remains, picked by C. Price (BM/NHM), and placed in separate trays awaiting accession at the NHM. The following accounts detail the previous work and herpetofaunal analyses.

TORNEWTON CAVE, DEVON

Tornewton Cave (NGR SX81726737) is situated about 250m to the southeast of Broken Cavern and Three Holes Cave. It was once almost filled with Pleistocene sediments. Extensive work by Widger, the Torquay Natural History Society and A.J. Sutcliffe (Sutcliffe and Zeuner, 1962) has emptied most of the sediments and revealed a top, a middle and a lower entrance (Roberts, 1996). The sedimentary sequence spans the whole Late Pleistocene and a significant part of the Late Middle Pleistocene.

Figures 6.15b and 6.18a shows the stratigraphic relationships between the deposits in Tornewton Cave. The Bear Stratum forms a thick layer in the main chamber, but is a rather thin unit in the adjacent Vivian's Vault, which is laterally discontinuous with the Bear Stratum in the Main Chamber. Throughout the Main Chamber, the Glutton Stratum underlies the Bear Stratum, but in Vivian's Vault, the Bear Stratum is underlain by the Otter Stratum.

Stuart (1982) previously recorded indeterminate anurans from the Bear Stratum. Holman (1990) recorded *R. temporaria* from a 'Wolstonian layer' in the cave, and it is assumed that this means the Glutton or Bear Stratum. The microvertebrate fauna from the Bear Stratum is of fully interglacial character and was most probably deposited during Substage 5e (Currant, 1996). This is consistent with observed differences in character from the overlying Hyaena Stratum, The Hyaena Stratum contains *M. oeconomus*, a typical element of later Stage 5 faunas, and is believed to occupy a considerable part of post-Ipswichian Stage 5, probably Substages 5c and 5a (Currant, 1996; Currant and Jacobi, 1997). The association of *Hippopotamus* remains with the Hyaena Stratum is problematic. However, Currant (1989) suggested the possibility that some *Hippopotamus* remains may have originally been associated with the Bear Stratum, but were wrongly attributed to the Hyaena Stratum. Herpetofaunal remains have been studied during the current project, from the Otter Stratum and the Hyaena Stratum.

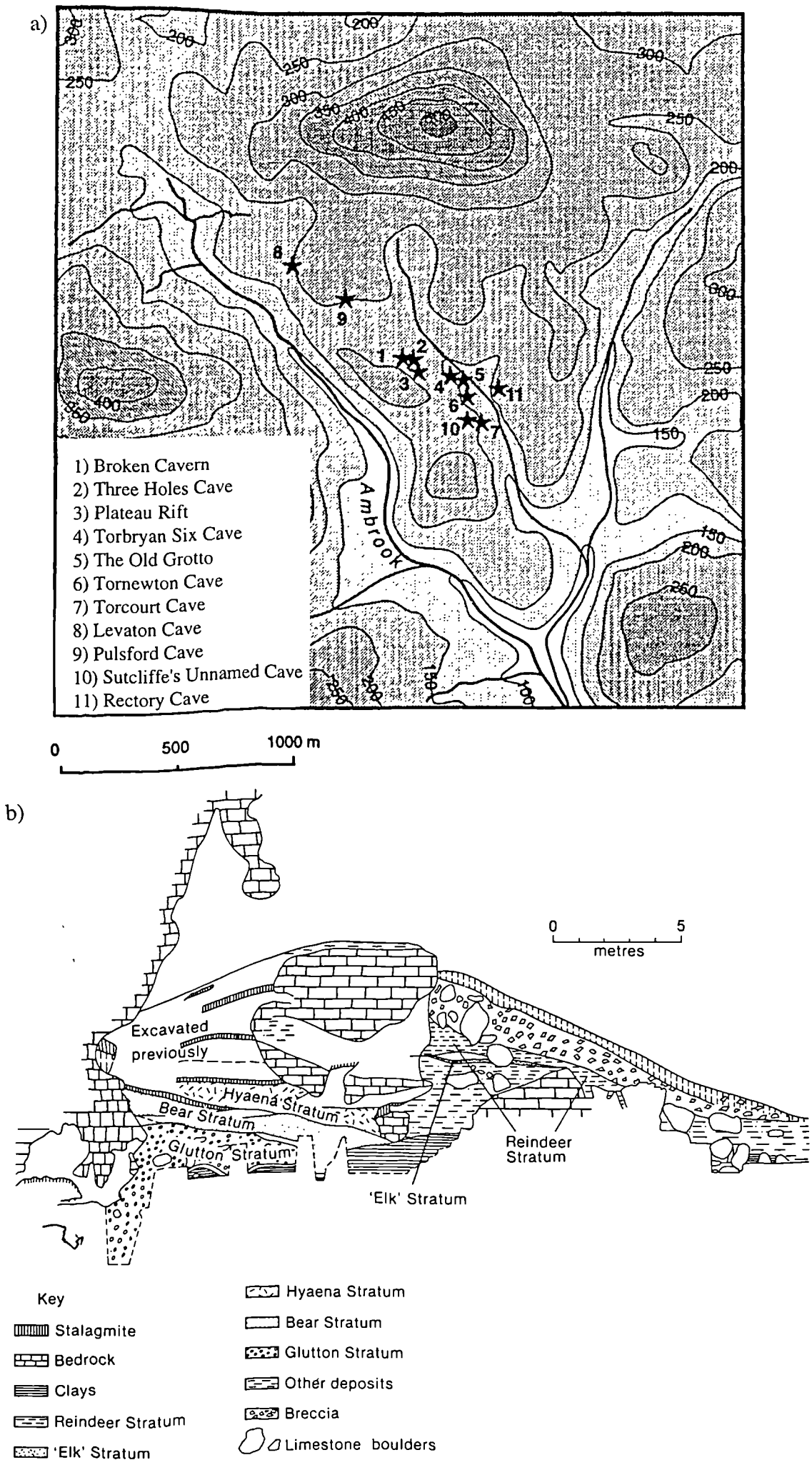


Figure 6.15: a) Location of the Torbryan Caves, Devon (after Roberts, 1996); b) Pleistocene lithostratigraphy of Tornewton Cave, Devon (modified from Sutcliffe and Zeuner, 1962).

OTTER STRATUM

A small amount of fragmentary material from the Otter Stratum was studied at the NHM during 1995. Unfortunately, no systematic descriptions were made, and the list given below only details the taxonomy of the material. There were very few fragments of recogniseable anuran material, and the species list is unlikely to be altered by re-appraisal, unless new material becomes available. Lithotratigraphically and biostratigraphically, the Otter Stratum appears to date to Stage 7 (Currant, 1996). The Otter Stratum is stratigraphically lower than the Bear Stratum (Substage 5e) in Vivian's Vault. It also contains abundant remains of *Crocidura* which is not known from any Last Interglacial sites, but is common at Stage 7 sites such as Aveley and Orsett Road, Essex, and Itteringham, Suffolk (Currant, 1996; Schreve, 1998). The remains are held at the NHM.

Systematic palaeontology

Bufo sp. indet.

Material. Several undeterminate fragments.

Rana sp. indet.

Material. Several undeterminate fragments.

Indeterminate Anura

Material. Several undeterminate fragments.

HYAENA STRATUM

The mammal fauna from the Hyaena Stratum indicates temperate conditions (Currant, 1996; Currant and Jacobi, 1997). Though it is reported to include *Hippopotamus*, the overall nature of the mammal fauna and its inclusion of *M. oeconomus*, suggest an age post-dating the Ipswichian maximum (Currant, 1996). Moreover, it lies above the Bear Stratum which is believed to belong to Substage 5e. As this unit comprises deposits laid down over a long period of habitation by spotted hyaena *Crocuta crocuta*, correlation with a large part of Stage 5 (possibly encompassing Substages 5c and 5a) might be appropriate (Currant, 1996; Currant and Jacobi, 1997). The herpetofaunal material recovered is held at the NHM. The bones are archived and labelled with original field excavation sample numbers. The herpetofaunal list is as follows: *B. bufo, B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara,* Lacertidae indet., *A. fragilis, Natrix* sp. Table 6.3 shows the taxa recovered from each sample.

Table 6.3

TN91 #108:	*B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis*

TN92 #15:	*B. calamita,* Anura indet.
TN92 #113:	Anura indet.
TN92 #130:	*B. calamita, Bufo* sp., *Rana* sp.
TN92 #155:	*Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
TN92 #161:	*Rana* sp., Anura indet.
TN92 #248:	*Rana* sp.
TN92 #252:	*B. bufo, B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
TN92 #253:	*Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara*
TN92 #267:	*B. calamita, R. temporaria, Rana* sp., Anura indet., *A. fragilis, Natrix* sp.

Systematic palaeontology

Bufo bufo

Material. TN 92 #252. One left scapula. TN91 #108. One sacrum.

Remarks. The scapula has no fossa adjacent to the glenoid articulation. The sacrum is large, with one complete diapophysis, not as flared as in *B. calamita.*

Bufo calamita

Material. TN 92 #252. One left and one right ilium, two trunk vertebrae. TN92 #130. One left ilium. TN92 #267. One sacrum. TN92 #15. One second (axis) vertebra.

Remarks. TN92 #252. Left ilium is incomplete, with the ala missing (see Figure 6.7a). Tuber is triangular and pyramidal, with a medial ridge ascending to its apex. Pars descendens is not wide, but is angled ventrally. Acetabular margin strongly overhanging. This ilium was submitted to the Oxford Radiocarbon Accelerator Unit for dating, with the expectation of obtaining an infinite date on it. Unfortunately, this determination failed through lack of datable material (P. Pettitt, pers. comm., 1997). The right ilium is similarly incomplete. The tuber rises sharply, with a strong medial ridge, and is pyramidal in form. Pars descendens relatively narrow, but angled ventrally. Both of these specimens have tubers of a different form to the sharply pointed ones found in many of the specimens from Ightham and Cow Cave. TN92 #15. The axis vertebra has very short diapophyses and a very wide anterior cotyle, for articulation with the flared condyle of the atlas in *B. calamita.*

Bufo sp. indet.

Material. TN #155. One partial tibiofibula. TN92 #130. One atlas vertebra. TN92 #252. Two right ilia and two trunk vertebrae. TN92 #253. Two partial tibiofibulae. TN91 #108. One left

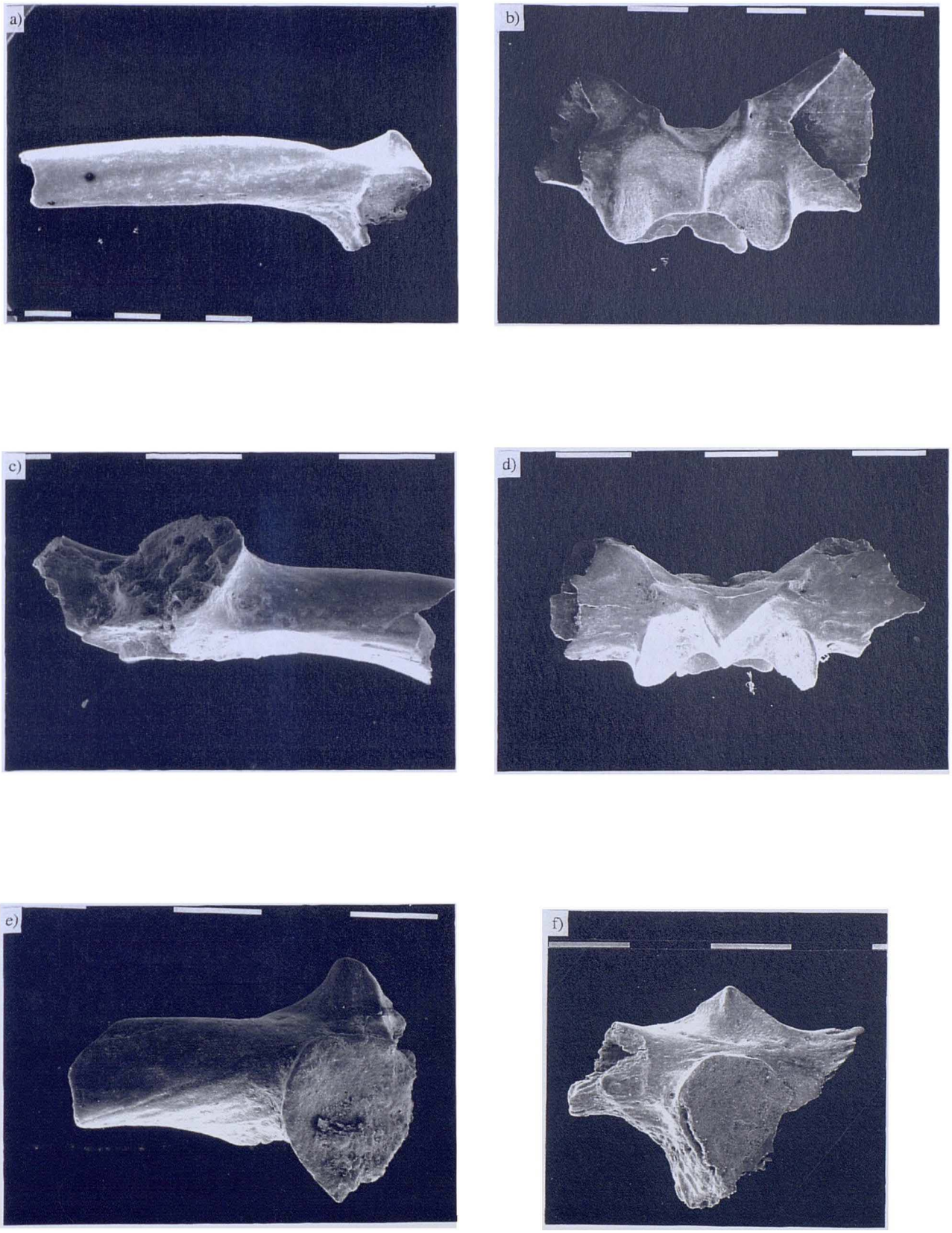


Figure 6.16: Remains of *B. calamita* from Hyaena Stratum, Tornewton Cave (a-b), Hyaena Den, Wookey Hole (c-e), and Sutton Courtenay (f): a) left ilium, lateral view (sample TN92 130); b) sacrum, dorsal view (sample TN92 267); c) left scapula, anterior view (sample HDH(S') H14+I14A); d) sacrum, dorsal view (sample 'South F'); e) left ilium, lateral view (sample H14/I14C); f) left ilium, lateral view (sample SC2/3).

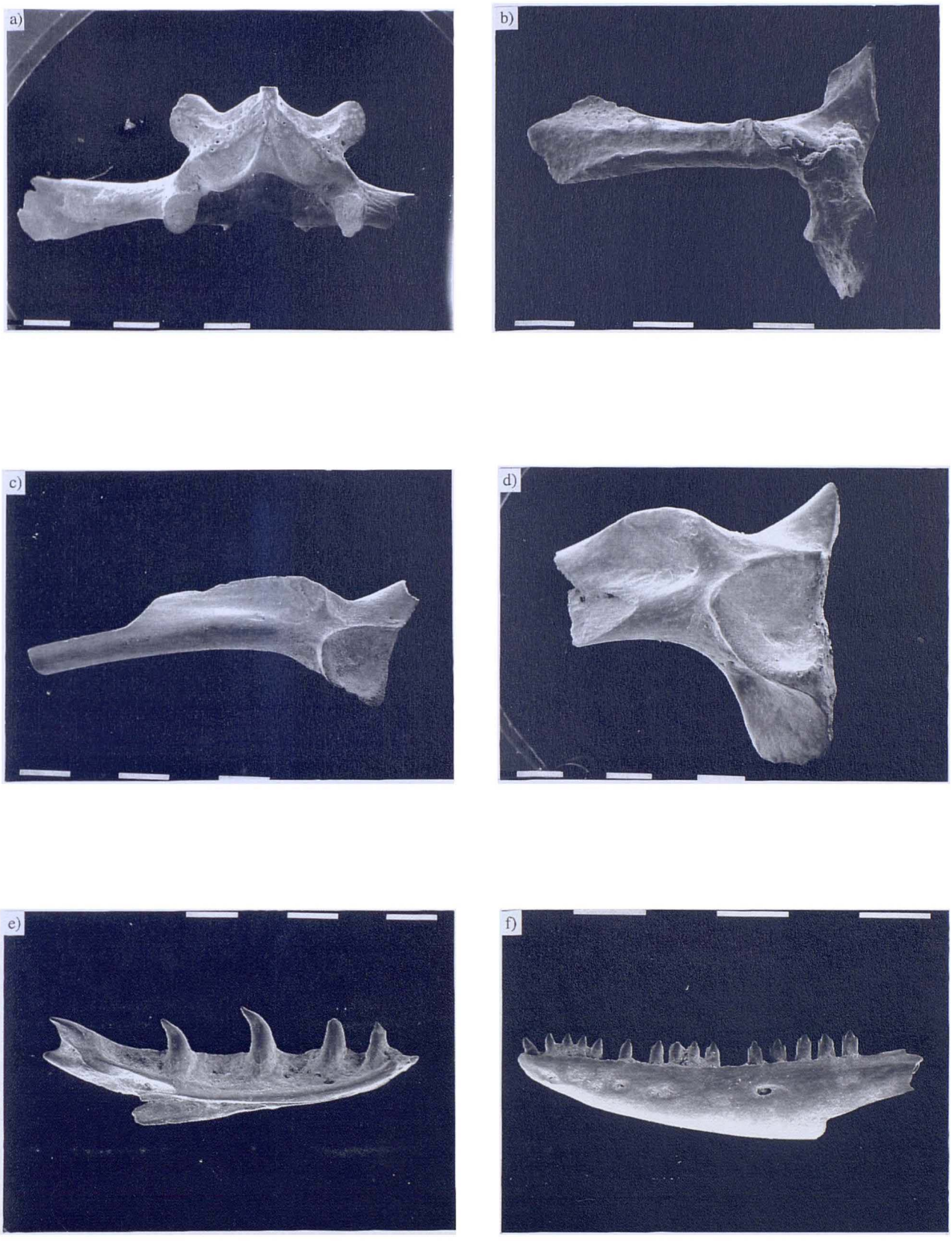


Figure 6.17: Herpetofaunal remains from Hyaena Stratum, Tornewton Cave: a) third vertebra (dorsal view) of *Rana* sp. cf. brown frog (sample TN91 108); b) right squamosal (medial view) of *Rana* sp. (sample TN92 253); c) left ilium (lateral view) of *Rana* cf. *temporaria* (sample TN92 253); d) left ilium of *R. temporaria* (sample TN91 108); e) left dentary (medial view) of *A. fragilis* (sample TN 91 108); f) left dentary (lateral view) of cf. *L. vivipara* (sample TN91 108).

humerus.

Remarks. TN92 #130. The atlas has a widely flared posterior central articulation, resembling *B. calamita*, but that diagnosis is not certain. TN92 #252. The right ilia are incomplete, with damaged tubers. Insufficient diagnostic characters are visible for specific identification. TN91 #108. the humerus is partly crushed, possibly during life.

Rana temporaria

Material. TN91 #108. One male left humerus, two third trunk vertebrae, one left and two right ilia. TN92 #253. Two left ilia. TN#155. One left and two right ilia. TN92 #252. Four left and three right ilia, and one right humerus. TN92 #267. One partial right ilium.

Remarks. TN91 #108 and TN92 #253. The ilia have strong tubers, which are steep and ribbed. Their vexillums are long and not as depressed as some recent specimens, but they are thick and strongly medially deflected. TN92 #253. One of the ilia (Figure 6.17c) has a relatively thin vexillum, and a fairly slender, tapering tuber compared to those referred to *R. temporaria*, from this site. There is a deep pre-acetabular fossa, and a deeply excavated supra-acetabular fossa, forming a sharp crista at its dorsal margin. It is distinct enough to warrant separation from the other ilia described above, and may be a different morph of *R. temporaria*. TN#155 and TN92 #252. These ilia have relatively shallow-sloping tubers with clear ribbing. The vexillum slopes neatly down from the tuber, becoming medially-deflected and thicker along the anterior parts of the ala. TN92 #267. This partial ilium has a relatively high and thin vexillum, and though only part of the tuber is intact, it appears to be slender. These third vertebrae have strong neural spines tapered into a posteriorly directed tubular crest. The transverse processes of one are also long, and widened towards the tips; the other is poorly preserved.

Rana sp. indet.

Material. TN92 #253. One right squamosal, eight trunk vertebrae, two sacra and a sacral fragment, one male II metacarpal, one sternum, seven partial tibiofibulae, two scapulae and one metapodial. TN#155. Two femora, eight partial tibiofibulae, one coracoid, one left scapula and one right angulosplenial. TN92 #130. One sacrum, one femur and one partial tibiofibula. TN92 #252. One right scapula, one radioulna, one femur, two tibiofibulae, one male II metacarpal, one trunk vertebra and three sacra. TN92 #248. One metapodial and two maxillary fragments. TN92 #267. Three trunk vertebrae, two sacra, one femur, three partial tibiofibulae, one metapodial, one right maxilla and one left scapula. TN92 #161. One partial tibiofibula and one partial right squamosal. TN91 #108. Two femora, two tibiofibulae, one pathogenic tibiofibula, one radioulna, one coracoid, two right scapulae, one sternum, one right angulosplenial, two tibiales, two fibulares, two metatarsals, three trunk vertebrae and one right maxilla.

Remarks. TN92 #253. The squamosal (Figure 6.17b) does not have a long anterior arm, but this appears to be broken, and the bone is encrusted in stalagmite. The lower tip is clearly

sharpened, with three corners, and the middle point protrudes well below the adjacent corners. These characters suggest that these elements may belong to a green frog. However, as vertebrae of *Rana* display such a high degree of variability, a firm referral can not be made. The lower end may also be damaged, giving a false impression of its original shape. The ilium has a fairly high tuber, with a faceted appearance, and only weak incisions rather than strong ribs. The vexillum is thin and blade-like, and is strongly deflected medially. Its junctura is very thin and in some ways it has the appearance of *R. arvalis* or *dalmatina*. TN92 #161. This squamosal has its dorsal part missing, its lower tip is fairly rounded but has a sharp point, thus it is not clearly distinguishable as green or brown frog.

Indeterminate Anura

Material. TN#155. One urostyle, three humeri and one radioulna. TN92 #15. One radioulna. TN92 #252. Three trunk vertebrae, four left and three right humeri, three radioulnae, one urostyle, one right scapula, two vertebral fragments and three ischia. TN92 #253. Two humeri, three radioulnae, one right pterygoid, one iscium, one urostyle, two coracoids, one partial vertebra, one partial tibiofibula and one phalanx. TN92 #267. One urostyle, one left angulosplenial, one right exoccipital, one metapodial and one phalanx. TN92 #161. One partial metapodial. TN92 #113. One partial radioulna. TN91 #108. Two radioulnae, one right angulosplenial, one coracoid, two metatarsals, seven metapodials and phalanges, one partial femur, one partial tibiofibula and one vertebral fragment.

cf. *Lacerta vivipara*

Material. TN91 #108. One left dentary, one right maxilla and two maxillary fragments.

Remarks. The dentary is shown in Figure 6.17f. These elements closely resemble modern *L. vivipara*.

Indeterminate Lacertidae

Material. TN92 #253. Two humeri.

Remarks. These are apparently lacertid and compare well with modern *L. vivipara*, but a more specific referral is not possible.

Anguis fragilis

Material. TN92 #267. One anterior part of a caudal vertebra. TN91 #108. One trunk vertebra, four caudal vertebrae, one partial caudal vertebra and one left dentary.

Remarks. Figure 6.17e shows the dentary.

cf. *Natrix natrix*

Material. TN92 #267. One partial trunk vertebra.

Remarks. The neural arch and spine are missing, thus only the ventral part of the vertebra (including the centrum) is left intact. The hypapophysis is broken, but was clearly produced into a spine (cf. *Natrix* and *Vipera*) rather than a flat keel. Referral to genus is difficult, however. If it belongs to *Natrix*, the broken left prezygapophyseal process seems to have been angled laterally as in *N. natrix* rather than anterolaterally as in *N. maura* and *N. tessellata*. It also seems too broad at its base to be *Vipera*. The thickened (swollen) posterior lateral neural walls also match modern *N. natrix* more than *V. berus*. Fine differences which are difficult to quantify, in the ventral morphology of these two species, also seem to point towards referral to *N. natrix*.

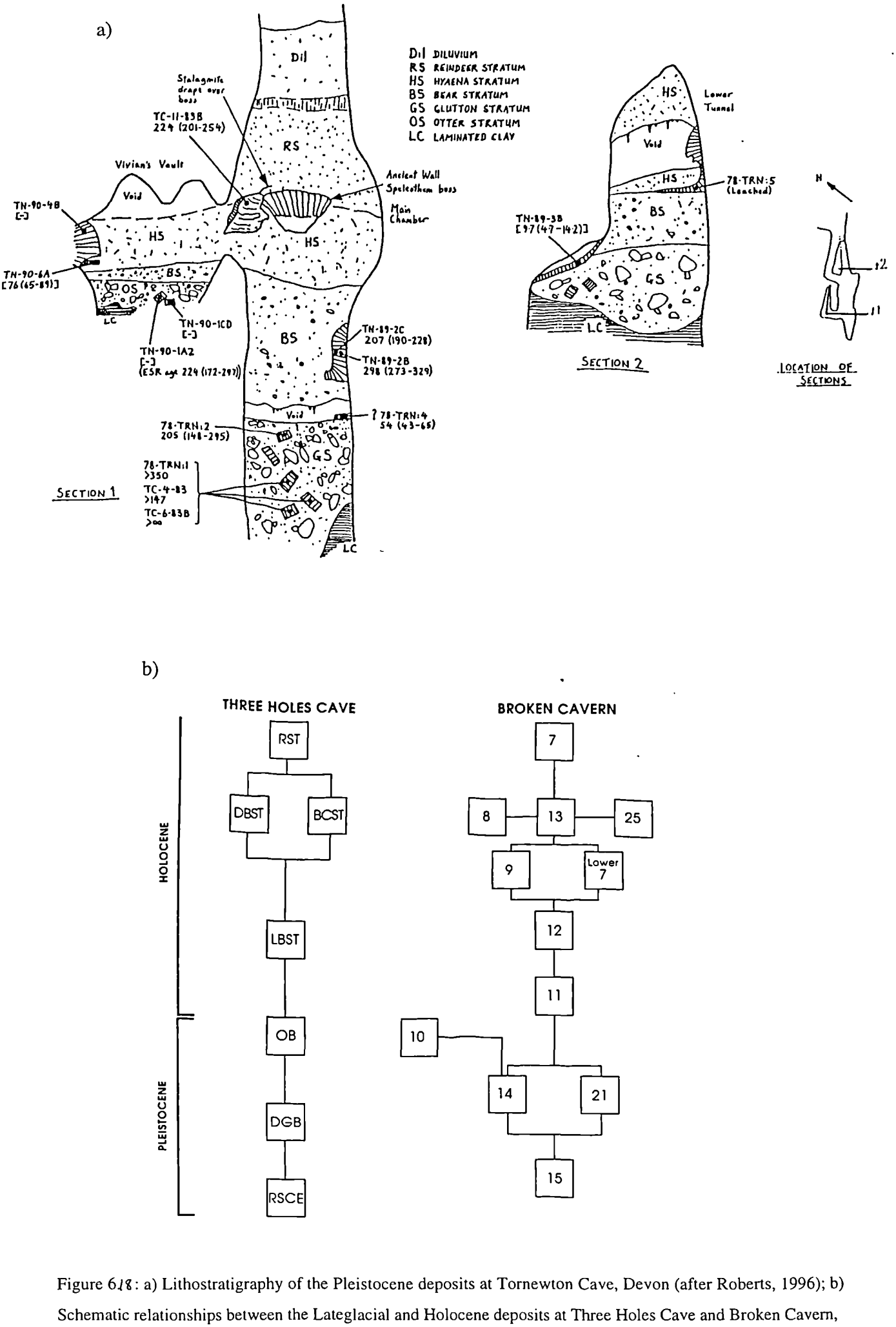


Figure 6.8: a) Lithostratigraphy of the Pleistocene deposits at Tornewton Cave, Devon (after Roberts, 1996); b) Schematic relationships between the Lateglacial and Holocene deposits at Three Holes Cave and Broken Cavern, Devon (after Roberts, 1996).

BROKEN CAVERN

Broken Cavern (NGR SX814676) is a collapsed cave which now forms a rockshelter (Roberts, 1996). It is situated 10m northwest of Three Holes Cave. It was first investigated by Widger who excavated the entrance area and recovered Neolithic implements. Most of the sediments investigated by the recent BM project are valley side sediments adjacent to the cave entrance (A.P. Currant, pers. comm.). A sketch section is shown in Figure 6.19. The stratigraphic relationships between the deposits at Broken Cavern are shown schematically in Figure 6.18. A long sequence of grey/green silts (Context 15) underlies Lateglacial Interstadial horizons. It has been dated by thermoluminescence (TL) and optically stimulated luminescence (OSL) to the 'end of the Last Glacial Maximum' (Roberts, 1996). Away from the cave wall, beneath early Holocene sediments, Contexts 14 and 21 contain Final Palaeolithic flints and charred mammal bones. A date of 11,380±120 ^{14}C BP (OxA-3887) on arctic hare was obtained from Context 21 (sample BRK #500), in association with the occupation horizon (Barton in Roberts, 1996). A large amount of angular limestone scree and boulders accumulated in the shelter, probably during the Younger Dryas (Roberts, 1996). At the back of the cave, the tufaceous Context 10 contained wolf bones and gnawed reindeer remains, consistent with use as a wolf den. An AMS radiocarbon date of 10,950±95 ^{14}C BP (OxA-3888) on wolf bone from this context falls within the currently accepted limits of the Younger Dryas stadial (Roberts, 1996). Overlying this unit is 2m of stony cave earth and talus (Contexts Lower 7, 9, 11, 12), dating to the early Holocene. It contains abundant 'environmental' evidence but no archaeology. Context Lower 7 appears to have resulted from dripline erosion of perched sediments above, and includes both early and middle Holocene woodland taxa and Lateglacial cold elements (Price in Roberts, 1996). Contexts 8, 13 and 25 have Neolithic and Bronze Age archaeology, and can thus be allocated a middle Holocene age. Indeterminate bone from Context 25 has been AMS dated to 4,650±70 ^{14}C BP (OxA-3889) (A. Roberts, pers. comm., 1998). Towards the western cave wall, Neolithic deposits are overlain by the Romano-British (c.2,000-1,500 BP) Context 7 Upper.

The small mammal fauna from Broken Cavern (Price, pers. comm., 1995; Price in Roberts, 1996) includes collared lemming, northern vole and mountain hare from Lateglacial Context 14. Several early to middle Holocene woodland indicators, such as bank vole and wood mouse, appear to have become partly admixed within Context 14 due to roof collapse (Price in Roberts, 1996). Several AMS dates on small mammals indicating different environments confirm the mixed nature of Context Lower 7: steppe pika 10,180±90 ^{14}C BP (OxA-4374), northern vole 10,370±90 ^{14}C BP (OxA-4375) and bank vole 5,770±75 ^{14}C BP (OxA-4496) (Price in Roberts, 1996). Bird remains include fieldfare, a modern winter visitor, from Context 21 (Stewart in Roberts, 1996). Early Holocene units produced grey partridge and (undeterminate) thrushes, larks and finches, together indicating the presence of at least some open grassland. Several fish species, including eel and a salmonid, are interpreted as being early colonisers (presumably at both caves) during the

Figure 6.19: Sketch section of the Lateglacial and Holocene deposits at Broken Cavern, Devon (after S. Collcutt, unpublished).

Lateglacial (Irving in Roberts, 1996). Three-spined stickleback, mullet and possibly nase (a primary freshwater cyprinid) were identified from Lateglacial Context 14 (sample BRK #370), the latter requiring a freshwater link between France and southwest England in order to colonise (Irving, pers. comm., 1995; Irving in Roberts, 1996). Molluscan remains from the caves generally support the biostratigraphic zonation scheme proposed by Kerney *et al* (1980), except that *Leiostyla anglica* appears to have reached Torbryan somewhat earlier than its first appearance in Kent (Seddon in Roberts, 1996). Closed canopy and shade species, probably correlating with biozone D2 (Kerney, 1977), include *Acicula fusca, Clausilia bidentata* and *Oxychilus cellarius*. Charcoal from a Late Upper Palaeolithic occupation horizon (Context 14) demonstrates the presence of ash and hazel (Cartwright in Roberts, 1996). Early Neolithic horizons (Contexts 8 and 13) yielded ash, field maple, oak, hazel, scots pine and ivy, together indicating a similar woodland cover to that found in the area today. Charcoal in Romano-British horizons identified the presence of the additional species hornbeam, birch and willow, though oak was not included. Pollen preservation is poor at both Broken Cavern and Three Holes Cave, and the few grains counted add nothing to the environmental picture given by the charcoal (Caseldine and Hatton in Roberts, 1996).

The herpetofaunal remains recovered from Broken Cavern are discussed below. A total of twenty-four samples produced herpetofaunal remains. The full assemblage is: *T. helveticus, T. vulgaris/helveticus, B. calamita, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V.* cf. *berus,* Ophidia indet. Table 6.4 shows the taxa recovered from each context and sample.

So far, three AMS Radiocarbon determinations have been successfully carried out by Oxford University Radiocarbon Accelerator Unit, on *B. calamita* bones from Broken Cavern. These were the first attempts by the Oxford Unit at obtaining AMS ages from amphibian remains. Using Stuiver and Reimer's (1993) 'CALIB 3', calibrated dates have also been calculated. Two partial scapulae from Context 21 (sample BRK #500) gave an age of 11,080±220 ^{14}C BP (OxA-6292), converting to 12,992 cal BP. Two left scapulae from Context 14 (sample BRK #243) gave an age of 10,850±90 ^{14}C BP (OxA-6991), or 12,775 cal BP. A right scapula (Figure 9.1a) from Context 11 (sample BRK #337) gave an age of 10,420±120 ^{14}C BP (OxA-6993), or 12,323 cal BP. These ages support the presumed ages indicated by archaeology, fauna and stratigraphy and closely fit the existing dates from the same contexts. The implications for biogeography and palaeoenvironmental reconstruction are discussed in Chapters 8 and 9. An AMS date on three *A. fragilis* vertebrae from Context 25 (sample BRK #525) gave an age of 4,430±60 ^{14}C BP (OxA-6954), and two *V. berus* vertebrae from Context 13 (sample BRK #409) gave an age of 4,540±65 ^{14}C BP (OxA-6953). Both dates are centred around the Neolithic-Bronze Age boundary, in close agreement with the archaeology and almost exactly matching the previous date from Context 25.

As four of the five Radiocarbon samples were composite (i.e. two or three bones from one

sediment sample), it could be argued that the dates are 'averages', and that their accuracy and validity could be questioned. However, individual field sampling was not vertically extensive, and with such close agreement with the archaeological age estimates, it is difficult to find reason to doubt the AMS ages. The only slight problem might be that the *B. calamita* date of 10,850±90 ^{14}C BP (on two left scapulae from Context 14, sample BRK #243) appears to fall after the supposed start of the Younger Dryas. It is possible that the two bones were of different ages and thus produced an average age (in which case one is older than the Younger Dryas and one is younger), or the accuracy of the dating technique could be questioned. Alternatively, the age estimation may be an accurate one. The palaeoclimatic indications are discussed in Chapter 9.

Table 6.4

Context Upper 7 (Romano-British - late Holocene)	
BRK #348:	*Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara*, *A. fragilis*
Grey tufaceous stalagmite (Neolithic, c.4.8-5.0ka BP - middle Holocene)	
BRK #407:	*A. fragilis*
BRK #430:	*A. fragilis*
Context 8 (Early Neolithic - middle Holocene)	
BRK #44:	*A. fragilis*
BRK #172:	*A. fragilis*
Context 13 (Early Neolithic - middle Holocene)	
BRK #409:	*B. bufo*, *Bufo* sp., *Rana* sp., Anura indet., *A. fragilis*, *V. berus*
Context 25 (Early Neolithic - middle Holocene)	
BRK #525:	*T. helveticus*, *T. vulgaris/helveticus*, *B. bufo*, *A. fragilis*, *V.* cf. *berus*
BRK #526:	*A. fragilis*, *V.* cf. *berus*
BRK #527:	*B.bufo*, *B. calamita*, *Bufo* sp., *R. temporaria*, *Rana* sp., Anura indet., *A. fragilis*, *V.* cf. *berus*
Context Lower 7 (early to middle Holocene)	
BRK #203:	*R. temporaria*, *Rana* sp., Anura indet.
Context 9 (early Holocene)	
(No herpetofaunal remains)	

Context 12 (early Holocene)
(No herpetofaunal remains)

Context 11 (early Holocene)
BRK #334A (0.638): *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
BRK #334A (0.688): *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
BRK #337: *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.

Context 10 (Lateglacial Stadial)
BRK #250: *Rana* sp., Anura indet., *A. fragilis*

Context 14 (Lateglacial Interstadial)
BRK #224: *B. calamita, Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara*
BRK #243: *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, V. berus,* Ophidia indet.
BRK #339: *Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
BRK #340: *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
BRK #346: *Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V. berus*
BRK #347: *Rana* sp., Anura indet.
BRK #370: *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.

Context 21 (Lateglacial Interstadial)
BRL #500: *B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.

Context 15 (Lateglacial)
BRK #254: *Rana* sp., Anura indet., cf. *L. vivipara*

Systematic palaeontology

Triturus helveticus

Material. BRK #525. Two caudal vertebrae.

Triturus vulgaris/helveticus

Material. BRK #525. One trunk vertebra.

Remarks. BRK #525. The neural spine is flat-topped but could be either species.

Bufo bufo

Material. BRK #527. Two left ilia, one right scapula and one partial right scapula. BRK #348. One left frontoparietal. BRK #409. Two partial right ilia, one left quadratojugal and one sphenethmoid.

Remarks. BRK #527. One ilium has a particularly large, elongate tuber. It consists of a long, sharp ridge extending from the ala to the pars ascendens, with its lateral face having a pair of parallel protrusive ridges. The pars descendens is very narrow and the corpus is thick.

Bufo calamita

Material. BRK #500. Four left and two right ilia, two scapulae, one left and one right incomplete frontoparietal-prootic, three left and two right radioulnae, one tibiofibula, three partial tibiofibulae and, two female left metacarpal III's, one partial urostyle and two trunk vertebrae. BRK #334A (x 0.688). One incomplete right scapula. BRK #337. One partial left and one right scapula. BRK #334A (x 0.638). One right ilium, one sacrum, one right scapula and one trunk vertebra. BRK #224. One partial left ilium, one trunk vertebra, one left and one right female metacarpal III. BRK #243. Two sacra, one left radioulna and three left scapulae. BRK #370. Two left ilia, one atlas, one partial tibiofibula and one left pterygoid. BRK #527. One right ilium and one right precoracoid. BRK #340. One right scapula and one partial right squamosal.

Remarks. BRK #500. Two partial scapulae were submitted for AMS radiocarbon dating (OxA-6292). One ilium is illustrated in Figure 6.21e. Its ala is partly missing, some of the pars descendens is missing. The tuber is not steeply ascending, but it is fairly pyramidal and has a well-defined apex. Subtle divergent lateral ridges can be seen as faint bumps in the lower flanks of the tuber. The ala is incomplete, but a strong ridge is apparent. The pars descendens is narrow, but partly missing. The angle between the ala and pars ascendens is very obtuse. The frontoparietals have their anterior (frontal) portions missing, but the parietal sections are distinctive and the prootics are attached. They are identical in size and though not associated, they appear to belong to the same individual. The radioulnae are thicker and more robust than *B. bufo*. Three have an obvious rib on their lateral side. The more complete specimens have a deep sulcus on their distal medial side between the radius and the ulna. The distal portion is flared. The size and shape of one is identical to the corresponding element in CGO 17/1. The tibiofibulae were identified by their cross-sectional shape and the sulcus associated with the nutritional foramen. The female metacarpals are robust and cylindrical, with tilted distal ends. They have the distinctive shape of *B. calamita* and belong to mature individuals. The urostyle is robust, with a low and very thick spine. BRK #334A (x 0.638). The ilium has a very obtuse angle of connection between the ala and corpus. The tuber has a rounded outline but has smooth lateral slopes. The ala is partly missing but there appears to have been a strongly developed blade. BRK #337. The right scapula was submitted for AMS radiocarbon dating (OxA-6993). BRK #527. The precoracoid has its medial end missing, but its lateral end is greatly flared (4mm wide). BRK #340. The squamosal is probably from a fairly small animal. Its ventral arm is missing but the dorsal region has a

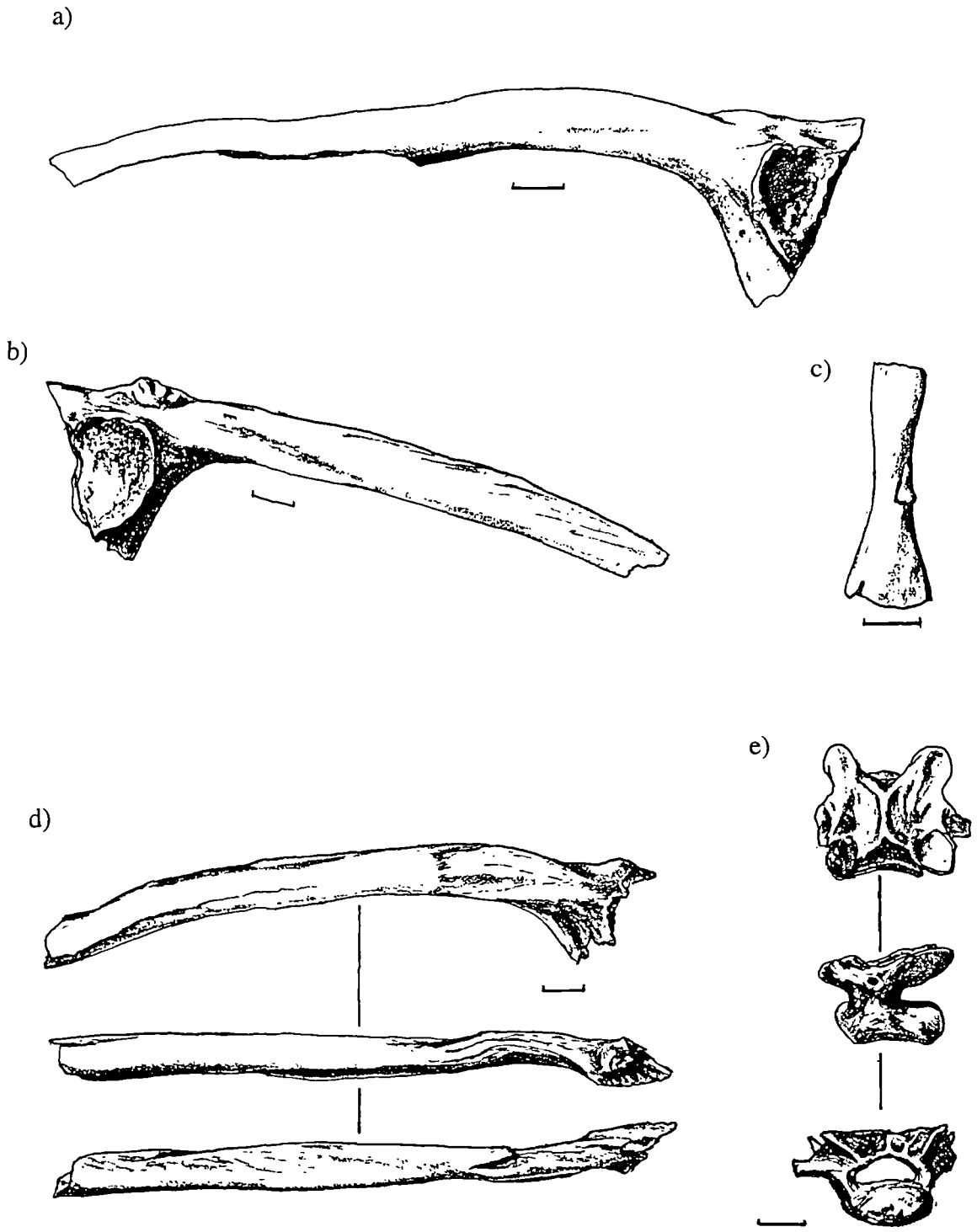


Figure 6.20 Anuran remains from Three Holes Cave (a-d) and Broken Cavern (e), Torbryan: a) left ilium of *B. bufo* (THR145); b) right ilium of *B. calamita* (THR150); c) male second digit metacarpal of *B.* cf. *bufo* (THR19); d) left ilium of *B. bufo*, with healed trauma injury (THR145); e) trunk vertebra of *B. calamita* (BRK224).

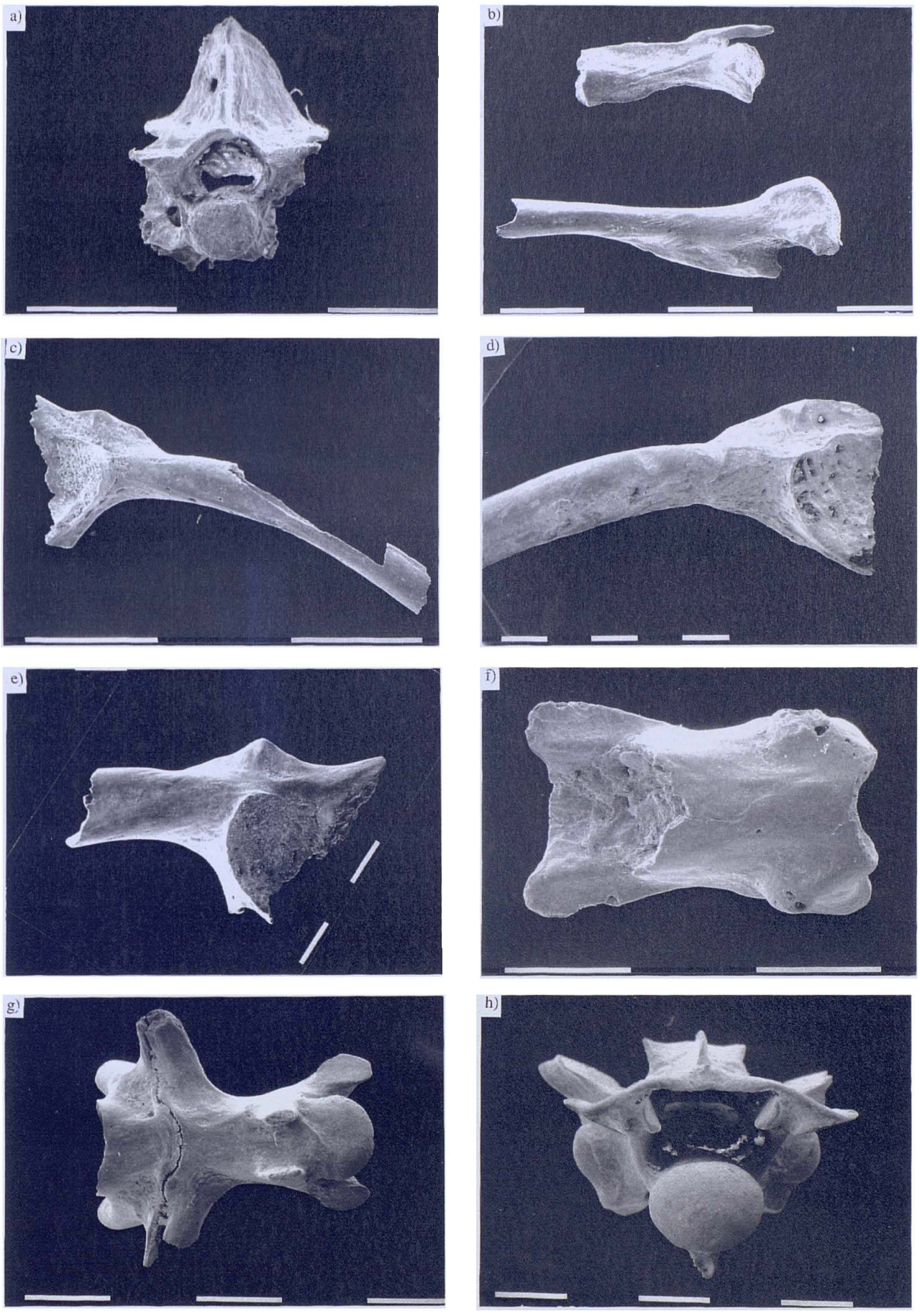


Figure 6.21: Herpetofaunal remains from Three Holes Cave (a,b,c,g) and Broken Cavern (d,e,f,h): a) trunk vertebra of *T. helveticus*, posterior view (THR 521); b) left femur and tibia of *Triturus* sp. (THR 327); c) juvenile left ilium of *B. bufo* (THR 521); d) left ilium of *B. bufo* (BRK 527); e) left ilium of *B. calamita* (BRK 500); f) trunk vertebra of cf. *L. vivipara*, ventral view (BRK 243); g) caudal vertebra of *A. fragilis*, ventral view (THR 327); h) trunk vertebra of *V. berus*, posterior view (BRK 409).

diagnostic shape. BRK #243. The sacra have their diapophyses mostly missing, but the V-shaped dorsal relief is diagnostic. Two of the left scapulae were submitted for AMS radiocarbon dating (OxA-6991).

Bufo cf. *calamita*

Material. BRK #337. One posterior trunk vertebra. BRK #500. One partial right angulosplenial, one partial left frontoparietal-prootic, two trunk vertebrae and one partial right coracoid. BRK #243. One right precoracoid, one trunk vertebra, three phalanges and one tibiofibula. BRK #370. One right pterygoid. BRK #340. One partial left ilium.

Remarks. BRK #500. The coracoid has its medial end missing, but it lateral end is broadly conical and ventrally expansive. The anterior and posterior edges of its constricted portion are sharply angular and its cross-section is exactly semi-circular. BRK #340. The ilium has much of the corpus and tuber missing. The tuber does not appear to have been particularly pointed, but it is not laterally protrusive and has a radial rib. The ala has a strong blade which breaks its outline when viewed laterally or dorsally.

Bufo sp. indet.

Material. BRK #334A (x 0.688). One tibiofibula. BRK #337. One tibiofibula, two radioulnae, five partial radioulnae, one partial coracoid, one partial precoracoid, one trunk vertebra, one proximal male metacarpal II and two phalanges. BRK #334A (x 0.638). One coracoid and two radioulnae. BRK #500. One trunk vertebra, two partial trunk vertebrae, one juvenile sacrum, one right humerus, one partial right humerus, one partial tibiofibula, one right coracoid, one metapodial, ten radioulnae and fragments thereof and one tibiale or fibulare. BRK #224. One partial right scapula, one partial right angulosplenial, one partial parasphenoid, three radioulnae, one female metacarpal III and one phalanx. BRK #243. One radioulna and one partial trunk vertebra. BRK #370. Three radioulnae, one femur, one right humerus, one precoracoid, two metacarpals and two phalanges. BRK #527. One partial right angulosplenial, one partial femur, one partial tibiofibula, one partial trunk vertebra, one left quadratojugal, one partial suprascapula, one phalanx and one partial long bone. BRK #348. One left angulosplenial. BRK #254. One partial left angulosplenial, one partial parasphenoid and one partial trunk vertebra. BRK #346. One trunk vertebra and one partial tibiofibula. BRK #340. Two femora, one trunk vertebra, one left coracoid, one right scapula and one metapodial. BRK #339. One right scapula, one femur and one partial tibiofibula. BRK #409. One partial left ilium, one male right humerus, two partial tibiofibulae, one partial trunk vertebra, one partial sacrum, one radioulna, one left premaxilla, one partial left angulosplenial, four phalanges and three distal phalanges.

Rana temporaria

Material. BRK #334A (x 0.688). One left and two right ilia. BRK #337. Three left and one

right ilium, one male left humerus. BRK #334A (x 0.638). One left and two right ilia, one male left and two male right humeri. BRK #500. Two partial left ilia. BRK #243. Two right ilia. BRK #370. One left and three right ilia and one juvenile right ilium. BRK #371.One right ilium. BRK #203. Two left and one right ilium. BRK #527. One left ilial ala. BRK #346. Two male left humeri. BRK #340. Four left and three right ilia. BRK #339. One left ilium and oe left ilial ala.

Remarks. BRK #346. One of the humeri has particularly well developed cristata, directed posteriorly and almost meeting medially.

Rana sp. indet. (brown frog)

Material. BRK #337. One male metacarpal II and one male left humerus. BRK #500. Two male left and one right humerus, one male metacarpal II and two tibiofibulae. BRK #243. One right frontoparietal. BRK #371. One male right humerus and one male metacarpal II. BRK #203. One male left humerus. BRK #346. One male left humerus. BRK #340. One male metacarpal II.

Rana sp. indet.

Material. BRK #334A (x 0.688). Three trunk vertebrae, one left and one right scapula, one partial right coracoid and one radioulna. BRK #337. Three radioulnae, three coracoids, one partial coracoid, three trunk vertebrae, two partial trunk vertebrae, one juvenile sacrum, one left and one right frontoparietal, two partial tibiofibulae, one femur, two partial left and one right angulosplenial, four left and two right humeri and three distal phalanges. BRK #334A (x 0.638). Two coracoids, two partial coracoids, one right scapula, one partial tibiofibula, two trunk vertebrae, one left and one partial right humerus. BRK #500. Four trunk vertebrae, one right angulosplenial, one partial right angulosplenial, three left and three right scapulae, one distal phalanx, two coracoids, one partial radioulna, three left and two right humeri, one right premaxilla and one female metacarpal II. BRK #224. One left scapula and one partial maxilla. BRK #243. One partial sacrum, one left coracoid, one radioulna, one partial femur, one partial tibiofibula, one partial right angulosplenial and one partial right scapula. BRK #370. Three left and two right ilia, three left and two right scapulae, two radioulnae, one trunk vertebra, one coracoid, six partial tibiofibulae, one left premaxilla, one partial premaxilla, one maxillary fragment, one partial right angulosplenial and one female metacarpal II. BRK #254. One left scapula and one partial right maxilla. BRK #347. One partial left and one partial right ilium, one left and one right scapula and one fragmentary maxilla. BRK #203. One coracoid, two partial coracoids, one partial left and one partial right ilium, one female left humerus, one partial radioulna and one partial trunk vertebra. BRK #527. One left scapula, one partial tibiofibula, one left premaxilla and one partial left maxilla. BRK #348. One left scapula, one metatarsal and one partial right angulosplenial. BRK #346. One partial left maxilla, two left humeri, one female right humerus and two radioulnae. BRK #250. One radioulna, one left scapula and one partial maxilla. BRK #340. One partial right ilium, one left squamosal, one right frontoparietal, one male partial left humerus, one femur, one partial

tibiofibula, one radioulna, two left and four right scapulae, two left premaxillae, three maxillary fragments, two trunk vertebrae, one sternum, one female metacarpal II and two metatarsals. BRK #339. One right coracoid, one left and one right scapula, one left angulosplenial, two right premaxillae and one maxillary fragment. BRK #409. One partial maxilla and one right carpal.

Indeterminate Anura

Material. BRK #334A (x 0.688). One male right humerus, four radioulnae, four vertebral fragments, three partial coracoids, four metapodials or phalanges and a long bone fragment. BRK #337. One urostyle, one partial coracoid, one partial right ilium, five vertebral fragments, one partial tibiofibula, one excoccipital, one ischium, one nasal, one partial frontoparietal, one partial suprascapula, one partial right pterygoid, one precoracoid, twenty-two metapodials or phalanges and fragments thereof. BRK #334A (x 0.638). One partial tibiale, one partial right scapula, one urostyle, one vertebral fragment and two partial phalanges. BRK #500. One humeral shaft, one partial left and one partial right humerus, one ischium, one partial parasphenoid, one left and one partial right angulosplenial, one right squamosal, one partial left squamosal, one partial femur, two prootics, one carpal,one partial femur, two partial tibiofibulae, two partial atlases, seventeen vertebral fragments, thirty-eight metapodials and phalanges and fragments thereof. BRK #224. Two partial right squamosals, two partial urostyles, one left dentary, one vertebral fragment and ten metapodials and phalanges. BRK #243. Two radioulnae, one partial urostyle, one vertebral fragment, one partial right squamosal, two metatarsals and one phalanx. BRK #370. One right exoccipital, one left angulosplenial, five radioulnae, one partial (pathological?) humerus, one right humerus, five vertebral fragments, two partial urostyles, one partial parasphenoid, one coracoid, one partial tibiofibula, one juvenile radioulna, twenty-one metapodials and phalanges and fragments thereof. BRK #254. One partial metapodial. BRK #347. One partial coracoid. BRK #371. One vertebral fragment. BRK #203. Three partial radioulnae, four vertebral fragments, one phalanx and five partial long bones. BRK #527. Five vertebral fragments, one partial radioulna, one metapodial and one phalanx. BRK #348. One partial tibiofibula, one partial coracoid, three phalanges and one partial metapodial or phalanx. BRK #346. Three radioulnae, two partial radioulnae, one partial right humerus and one partial metapodial or phalanx. BRK #250. One partial left ilium, two partial urostyles, one radioulna, two partial metapodials and one phalanx. BRK #340. One ischium, six radioulnae and fragments thereof, four vertebral fragments, one partial sacrum, two partial coracoids, one partial left and one partial right frontoparietal, one partial right pterygoid, six metapodials and phalanges. BRK #339. One partial left ilium, three radioulnae, one female right humerus, one tibiofibula fragment, one vertebral fragment, one partial urostyle, one indeterminate cranial fragment, eight metapodials and phalanges and fragments thereof. BRK #409. Five hyoidal cornua, one scapula fragment, one vertebral fragment, one metapodial, one metapodial fragment and two phalanges.

cf. *Lacerta vivipara*

Material. BRK #224. One right dentary. BRK #243. Twenty-one cervical and trunk vertebrae, two partial trunk vertebrae, one associated partial presacrum and sacrum, eleven sacral and cloacal vertebrae, one posterior half of a caudal vertebra and two right humeri. BRK #348. One cloacal vertebra. BRK #254. One trunk vertebra. BRK #346. One right humerus. BRK #254. One partial left humerus.

Remarks. BRK #224. This is a small specimen and its anterior tip and posterior portion are missing. It has only one tooth intact, but the arrangement of four external foramina is identical to *L. vivipara* CGO 41/1. BRK #243. Seven of the trunk vertebrae are particularly elongate and may belong to a female. One is illustrated in Figure 6.21f. Most of the vertebrae are of similar size or larger than CGO 41/1. One humerus is smaller than CGO 41/1, the other is of similar size. BRK #346. The humerus has a very slender, flat shaft and the distal epiphysis is missing. BRK #254. This is from a sub-adult animal. It is smaller than CGO 41/1 and the distal epiphysis is missing.

Anguis fragilis

Material. BRK #409. One quadrate, one partial cervical vertebra, seventeen trunk vertebrae, five partial trunk vertebrae, three ribs, one caudal vertebra, seven anterior halves of caudal vertebrae, four posterior halves of caudal vertebrae, and three hundred and fifty-three osteoderms. BRK #44. One osteoderm. BRK #407. One right frontal. BRK #525. Three trunk vertebrae, one caudal vertebra, one anterior half of a caudal vertebra and twelve osteoderms. BRK #526. Two trunk vertebrae. BRK #527. Four trunk vertebrae, one cloacal vertebra, three posterior halves of caudal vertebrae, one rib, one partial left maxilla, one partial parietal, one right postfrontal, one left dentary and eight osteoderms. BRK #348. One trunk vertebra, two caudal vertebrae and five osteoderms. BRK #172. One trunk vertebra. BRK #430. One osteoderm. BRK #346. One osteoderm. BRK 3250. One posterior half of a caudal vertebra.

Remarks. BRK #525. The three trunk vertebrae were submitted for AMS radiocarbon dating (OxA-6954).

Vipera berus

Material. BRK #409. Two trunk vertebrae and two partial trunk vertebrae. BRK #243. One partial trunk vertebra. BRK #346. One partial trunk vertebra.

Remarks. BRK #409. One trunk vertebra was submitted for AMS radiocarbon dating (OxA 6953). The remaining vertebra has a low neural arch (see Figure 6.21h), its hypapophysis is broken but is clearly acutely tapered. The partial specimens have their hypapophyses elongate and acutely pointed, extending well beyond the articular condyle. BRK #243 and BRK #346. Only the posterior articular condyle and hypapophysis are intact, but these clearly belong to *V. berus.*

Vipera cf. *berus*

Material. BRK #409. Four trunk vertebrae and two partial trunk vertebrae. BRK #525. One trunk vertebra. BRK #526. One trunk vertebra. BRK #527. One trunk vertebra and one partial rib.

Remarks. BRK #409. These are viperine vertebrae and probably belong to *V. berus*. Their hypapophyses are broken and they otherwise lack conclusive diagnostic features.

Indeterminate Ophidia

Material. BRK #409. Four vertebral fragments. BRK #243. One partial trunk vertebra. BRK #408. One partial trunk vertebra.

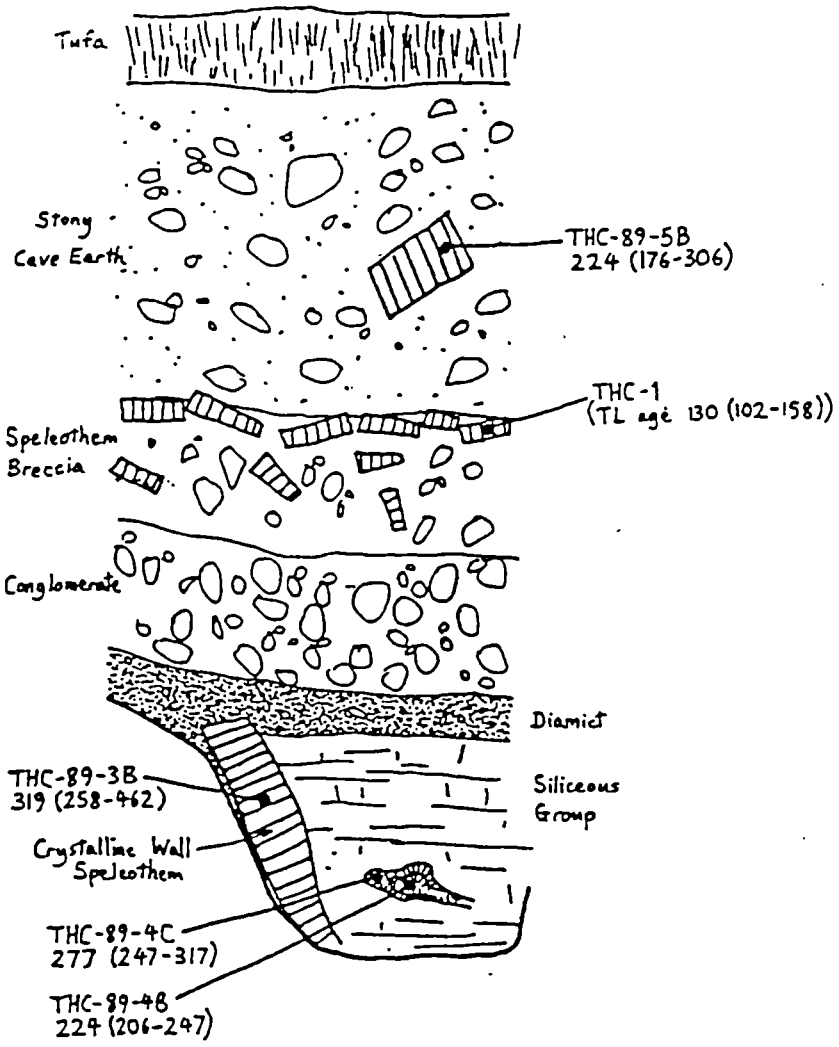
THREE HOLES CAVE

Three Holes Cave (NGR SX815676) consists of a short passage and a single chamber. The impression of holes in the cave roof, given by the presence of large limestone blocks near the surface, gave rise to the cave's name (Roberts, 1996). The cave is located 10m to the southeast of Broken Cavern, close to the Plateau Rift fissure with which it may once have been connected. Archaeological finds from the cave span most periods from the Middle Palaeolithic until the present. Recent work has concentrated on the entrance area and the chamber.

The four basic stratigraphic divisions suggested for Three Holes Cave by S. Collcutt (Robert, 1996) are: 1) Siliceous Group water-lain deposits; 1) Calcareous Group, post-dating the Siliceous Group and forming the majority of the deposits in the cave; 3) 'Hanging Deposits', consisting rounded breccias and conglomerates surviving from previous phases of sedimentation; 4) Crystalline Wall Speleothem, contemporary with the Siliceous Group or slightly younger, but pre-dating the Calcareous Group. The Calcareous Group can be subdivided into six units, of which the Stony Talus (Bed 6) is the most important. It forms a sloping sequence outside the cave entrance, and consists of various Holocene deposits, including five archaeological contexts (Roberts, 1996). Most of the samples which concern the recent archaeological and palaeontological work have thus come from the Stony Talus. Underlying the base of the Stony Talus, the Red Stony Cave Earth (RSCE) contains a Late Upper Palaeolithic hearth horizon (DGB). Six AMS dates on brown bear, horse, red deer and mountain hare centre around 12.2ka BP (Barton in Roberts, 1996). The layer is topped by a lens of sterile Orange Brown (OB) sediment which is presumably of Lateglacial Stadial age. Whereas the overlying Stony Talus occurs only outside the cave entrance, the cave earth continues inside the cave. The Holocene Stony Talus begins with the Light Brown Stony Talus (LBST), which contains Later Mesolithic archaeology and an unambiguously associated faunal assemblage (Roberts in Roberts, 1996). It is 20-30cm thick and overlain by 10-20cm of archaeologically sterile material. Radiocarbon determinations on red deer from this predated assemblage gave ages of 6,330±75 ^{14}C BP (OxA-4491) and 6,120±75 ^{14}C BP (OxA-4492) (Roberts in Roberts, 1996). Around the cave wall, a richly tufaceous deposit, the Grey Tufaceous Stony Talus (GTST), forms the lateral equivalent of the LBST. Above these units, extensive Neolithic human activity is evidenced by high charcoal contents in the sediments. The Black Charcoal-rich Stony Talus (BCST) extends c.5m out from the cave entrance and is surrounded by its lateral equivalent, the Dark Brown Stony Talus (DBST), which has a lower charcoal content. The associated mammal fauna was dominated by non-domesticated species such as aurochs, wild boar and roe deer. Two AMS dates on aurochs from the BCST produced ages of 5,060±70 ^{14}C BP (OxA-4493) and 5,010±70 ^{14}C BP (OxA-4495) (Berridge in Roberts, 1996). Above these layers, the Red Stony Talus (RST) forms the majority of the talus deposits and contains Bronze Age artefacts with some Late Neolithic at its base. A schematic representation of the deposits at Three Holes Cave is shown in Figure 6.22.

Microfaunal remains from Three Holes Cave have undergone less disturbance and admixture

a)



b)

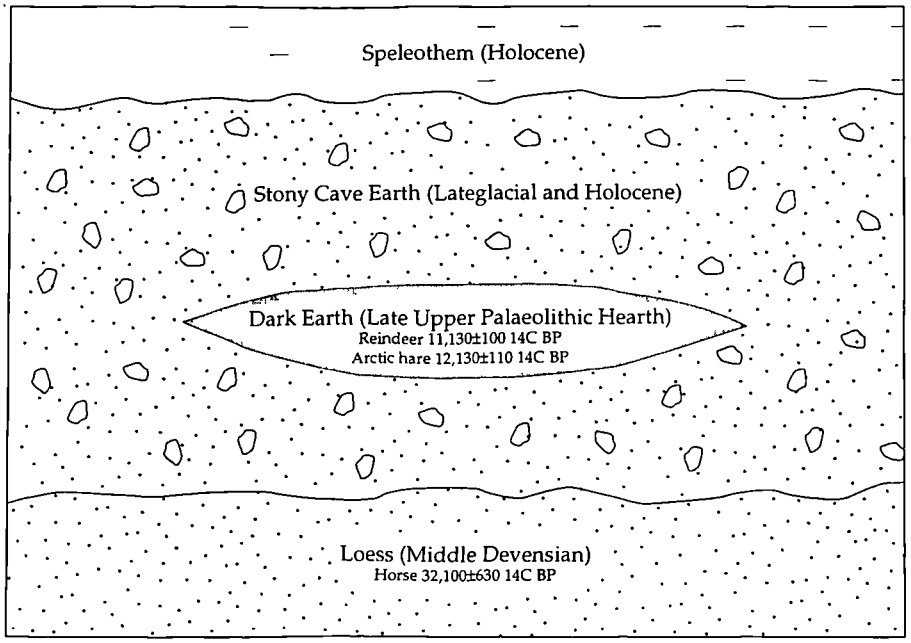


Figure 6.22: a) Lithostratigraphy of the Lateglacial and Holocene deposits at Three Holes Cave, Devon (after Roberts, 1996); b) Schematic representation of the Lateglacial and Holocene deposits at Torbryan Six Cave, Devon.

than at Broken Cavern, but compaction has caused more breakage (Price in Roberts, 1996). According to Stewart (in Roberts, 1996), none of the bird remains are identifiable for this reason. During the early Holocene, bank vole replaced field vole as the dominant small mammal species, as local woodland developed. Neolithic and Bronze Age layers yielded dormouse and red squirrel, indicating mature woodland with a thick understorey (Price in Roberts, 1996). There was no woodland clearance in the Torbryan Valley until at least the Romano-British period, and historical records show that it was wooded during Mediaeval times. Microfaunal accumulation was probably due to owls roosting above the cave entrance, a theory which is supported by concentrations of remains beneath the dripline (Price in Roberts, 1996). Molluscan remains from the Lateglacial hearth include *Acanthinula aculeata*, possibly indicating woodland locally (Seddon in Roberts, 1996), although many of the taxa from a Late Mesolithic horizon are shade-loving rather than being specific to woodland. Abundant charcoal fragments from Neolithic layers include remains of hazel, ash, blackthorn, field maple, oak, ivy, spindle, dog-rose, dogwood and elder, indicating an association of Rodwell's (1991) W8 woodland type (Cartwright in Roberts, 1996).

A total of sixty-three samples produced herpetofaunal remains. The full herpetofaunal list is: *T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara,* Lacertidae indet., *A. fragilis*. The species recovered from each sample and context are listed in Table 6.5 below.

Table 6.5.

RST: Red Brown Stony Talus (Bronze Age, Late Neolithic at base - Middle Holocene)	
THR #145:	*B. bufo, Bufo* sp., Anura indet.
THR #150:	*B. bufo, Bufo* sp.
THR #151:	*Bufo* sp.
THR #327:	*T. vulgaris/helveticus, B. bufo, Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis*
RST/DBST (Later Neolithic - middle Holocene)	
THR #530:	*B. bufo, Bufo* sp.
THR #531:	*B. bufo, Bufo* sp., *A. fragilis*
RST/BCST (Later Neolithic - middle Holocene)	
THR #174:	*B. bufo*
THR #175:	*Bufo* sp.
DBST: Dark Brown Stony Talus (Neolithic - middle Holocene)	
THR #348:	Anura indet.

THR #349: *Bufo* sp., *Rana* sp., Anura indet., *A. fragilis*
THR #350: *B. bufo, Bufo* sp., Anura indet., *A. fragilis*
THR #445: Anura indet.
THR #537: *B. bufo, Bufo* sp., *A. fragilis*
THR #538: Anura indet., *A. fragilis*

BCST: Black Charcoal-rich Stony Talus (Neolithic - middle Holocene)
THR #325: *Bufo* sp., Anura indet., *A. fragilis*
THR #343: *Bufo* sp., Anura indet., *A. fragilis*
THR #347: *A. fragilis*
THR #443: Anura indet.
THR #451: *Bufo* sp., Anura indet.
THR #457: cf. *L. vivipara, A.fragilis*
THR #493: *Bufo* sp.
THR #496: *Bufo* sp.
THR #497: *A. fragilis*
THR #506: *B. bufo,* Anura indet.
THR #541: *Bufo* sp.
THR #542: *Bufo* sp.
THR #543: *Bufo* sp., Anura indet.

DBST-BCST (Neolithic - middle Holocene)
THR #345: *T. vulgaris/helveticus, B. bufo, Bufo* sp., Anura indet., *A. fragilis*
THR #346: *B. bufo, R.* cf. *temporaria, Rana* sp., Anura indet., *A. fragilis*
THR #351: *B. bufo, Bufo* sp., Anura indet., *A. fragilis*
THR #354: *B. bufo, Bufo* sp., *Rana* sp., Anura indet., *A. fragilis*

GTST: Grey Tufaceous Stony Talus (above LBST at cave wall - middle Holocene)
THR #31: *B. bufo, Bufo* sp.
THR #41: *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.

BCST/LBST (Mesolithic to Neolithic? - middle Holocene)
THR #498/499: *Bufo* sp., *A. fragilis*
THR #535: *A. fragilis*

LBST: Light Brown Stony Talus (Later Mesolithic, ^{14}C dates c.6.3ka BP - middle Holocene)
THR #19: *Bufo* sp., Anura indet.
THR #53: *Bufo* sp., Anura indet.

THR #56:	*Rana* sp., Anura indet.
THR #67:	*Bufo* sp.
THR #71:	Anura indet.
THR #74:	*Bufo* sp., Anura indet.
THR #91:	*Bufo* sp., Anura indet.
THR #110:	Anura indet., *A. fragilis*
THR #118:	*Rana* sp., Anura indet.
THR #520:	*B. bufo, Bufo* sp., Anura indet, *A. fragilis*
THR #521:	*T. helveticus, Bufo* sp., Anura indet., *A. fragilis*
THR #533:	*Bufo* sp., Anura indet., *A. fragilis*

OB: Orange Brown lens (Lateglacial Stadial?)
(No herpetofaunal remains)

DGB: Dark Grey Black (LUP hearth, mean ^{14}C dates = 12.2ka BP - Lateglacial Interstadial)

THR #38:	*Bufo* sp.
THR #69:	*Bufo* sp.
THR #88:	*Bufo* sp., *R. temporaria,* Anura indet., Lacertidae indet., *A. fragilis*
THR #102:	*Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis*
THR #272:	Anura indet.
THR #340:	Anura indet.
THR #393:	*Bufo* sp., *Rana* sp.
THR #398:	Anura indet., *A. fragilis*
THR #406:	*Bufo* sp.

RSCE: Red Stony Cave Earth
(No herpetofaunal remains)

Systematic palaeontology

Triturus vulgaris/helveticus

Material. THR #345. One left scapulocoracoid. THR #327. One left femur and one left tibia.

Remarks. THR #345. This element is illustrated in Figure 6.21a. THR #327. These elements are illustrated in Figure 6.21b.

Triturus helveticus

Material. THR #521. One cervical vertebra.

Bufo bufo

Material. THR #327. One partial right ilium, one partial right frontoparietal, one partial frontoparietal. THR #530. One left precoracoid. THR #531. One right squamosal. THR #350. One left squamosal. THR #537. One right scapula. THR #381. One left and one right precoracoid. THR #31. One left ilium. THR #38. One right ilium. THR #145. One left ilium. THR #146. One partial right ilium. THR #146. Three left ilial alae. THR #174. One right ilium. THR #150. One right ilium and one male right humerus. THR #184. One left ilium and one fourth vertebra. THR #506. One right ilium. THR #520. One right scapula and one partial left scapula. THR #354. One left ilium. THR #346. One partial left scapula. THR #351. One partial right squamosal. THR #521. One larval left ilium.

Remarks. THR #350. The squamosal is from a large individual c.120mm. THR #145. The ilium is illustrated in Figure 6.21d. THR #146. Most of the corpus is missing, the tuber is low and rounded but recogniseable as *B. bufo*, and the ala is crushed flat. THR #146. These alae are from mature individuals, but lack any form of ventrolateral blade. THR #174. The ilium has its ala missing, and the break is polished. THR #150. The humeral shaft is narrow within the range of *B. bufo*, and is overall less robust than *B. calamita*. THR #521. The ilium is minute and must belong to a premetamorphosed larva (see Figure 6.21c).

Bufo sp. indet.

Material. THR #327. One ilial ala, one nasal, three male metacarpal II's, two tibiofibulae, one partial tibiofibula, one left squamosal, one partial squamosal, one right angulosplenial, two partial right ilia, one partial right suprascapula, one trunk vertebra, three radioulnae, one coracoid, sixteen metapodials and phalanges, one fibulare and one partial tibiale. THR #542. One male metacarpal II. THR #543. One femur. THR #349. One femur, one partial sacrum, one right dentary, two metapodials and a phalanx. THR #530. One partial metatarsal. THR #531. One phalanx. THR #350. One femur, two phalanges and two distal phalanges. THR #537. One phalanx and one left premaxilla. THR #88. One vertebral fragment, one partial tibiofibula, one partial fibulare, one left pterygoid, one metatarsal and one phalanx. THR #406. One metapodial. THR #393. One partial femur. THR #102. One partial tibiale, one distal phalanx and one partial squamosal. THR #31. One right humerus, three partial femora and one tibiale. THR #31. One partial right ilium. THR #69. One femur. THR #38. One right humerus, two radioulnae, one partial tibiofibula and one right ilial ala. THR #146. Two radioulnae, one tibiofibula, one left and one right humerus and one fibulare. THR #145. One left ilium, one partial radioulna, two femora, three tibiofiubulae and one female right humerus. THR #175. One humeral shaft. THR #151. One tibiofibula and one fibulare. THR #411. One partial femur. THR #383. One partial tibiofibula. THR #451. One radioulna and one phalanx. THR #345. One male partial right humerus, one male metacarpal II, one partial trunk vertebra, one left ilial ala, one partial ilial ala, one tibiofibula

fragment and one partial left suprascapula. THR #67. One partial left coracoid. THR #325. One right angulosplenial. THR #91. One tibiofibula. THR #74. One partial third vertebra. THR #19. One radioulna, one female left humerus, two male metacarpal II and one partial tibiofibula. THR #533. One phalanx. THR #53. One partial tibiofibula. THR #521. One partial femur and one radioulna. THR #520. One partial femur, one vertebral fragment, one radioulna, one male metacarpal II and one partial male metacarpal II. THR #354. One male left humerus, two left humeri, two partial femora, one right angulosplenial, one right premaxilla, one partial trunk vertebra and two phalanges. THR #351. One metapodial and one distal phalanx. THR #498/499. One phalanx. THR #493. One phalanx. THR #343. One distal manual phalanx. THR #496. One tibiale.

Remarks. THR #145. The left ilium (see Figure 6.20d) has part of the corpus missing, but the ala has a repaired trauma injury. Close to the junction with the corpus, the ala has been crushed and displaced medially. The fracture has not healed totally, but the pars descendens is expanded into a larger and thinner area than usual, cf. *Hyla*. This may be compensatory growth related to the trauma injury. The tuber is fairly pyramidal and pointed, but it is quite low and not equivocally *B. calamita* or *B. bufo*. The ala has a short but well developed ventrolateral ridge. The radioulna lacks its proximal end, but its dorsal margin is straight cf. *Bufo*. One of the tibiofibulae is polished around its broken end, in the mid-shaft region. THR #175. The broadly expanded proximal humeral shaft and the very produced anterior crista are characteristic of *Bufo*.

Rana temporaria

Material. THR #88. One male right humerus. THR #146. One left ilium and one right ilium.

Remarks. THR #146. The right ilium is illustrated in Figure 6.14a. It appears to have at least two puncture-type teeth marks in the tuber area.

Rana cf. *temporaria*

Material. THR #31. One incomplete male right humerus and one sacrum. THR #346. One male left humerus.

Remarks. THR #31. The sacrum has particularly robust diapophyses.

Rana sp. indet.

Material. THR #327. One sacrum, one juvenile sacrum and one trunk vertebra. THR #349. One left dentary and one metapodial. THR #88. One incomplete femur. THR #393. One metatarsal. THR #102. One sacrum and one partial male metacarpal II. THR #31. One radioulna and one femur. THR #146. One male right humerus, one female left humerus, one radioulna, five femora, two tibiales and one fibulare. THR #451. One pathological male metacarpal II. THR #118. One partial radioulna. THR #56. One partial sacrum. THR #521. One left angulosplenial. THR

#354. One juvenile metatarsal. THR #346. One juvenile sacrum.

Remarks. THR #348. This appears to be a particularly short pathological metacarpal. THR #118. The radioulna is very rolled or abraded.

Indeterminate Anura

Material. THR #327. One urostyle, eleven vertebral fragments, one right exoccipital, one partial pterygoid, two partial parasphenoids, two radioulnae, three partial precoracoids, two partial tibiales or fibulares, seventeen metapodials and phalanges. THR #543. One partial trunk vertebra. THR #349. One phalanx and one partial radioulna. THR #530. One right precoracoid and one metapodial. THR '89 Yellow clay 13.10.89. One partial metapodial or phalanx. THR #530. One vertebral fragment, one partial metapodial, four phalanges and one distal phalanx. THR #538. One vertebral fragment. THR #88. Two vertebral fragments, one coracoid, one quadratojugal and three indeterminate long bone fragments. THR #381. One indeterminate fragment. THR #398. One proximal partial phalanx. THR #272. One partial coracoid. THR #340. One fragmentary urostyle. THR #102. Two fragmentary vertebrae, one phalanx and two indeterminate fragments. THR #31. One humeral shaft. THR #146. One urostyle. THR #145. Three urostyles. THR #348. One vertebral fragment. THR #451. One vertebral fragment and one long bone fragment. THR #325. One partial urostyle, four phalanges and fragments thereof and four other indeterminate fragments. THR #541. One partial phalanx. THR #443. One phalanx and one distal phalanx. THR #118. One fragmentary long bone. THR #445. One partial pterygoid and one phalanx. THR #345. One sphenethmoid, one phalanx and two vertebral fragments. THR #506. One partial sacrum, one phalanx and one partial phalanx. THR #56. Two partial vertebrae, one phalanx and one partial exoccipital. THR #110. Two partial vertebrae and one vomer. THR #71. One phalanx. THR #91. One metapodial and one vertebral fragment. THR #19. Two partial vertebrae and one phalanx. THR #533. One partial phalanx. THR #53. One phalanx. THR #520. One partial vertebra and three phalanges. THR #354. Two partial trunk vertebrae, one hyoidal cornu, one partial parasphenoid, four phalanges and three fragments. THR #346. One metapodial, one phalanx and one vertebral fragment. THR #351. One partial vertebra and three phalanges. THR #343. One partial phalanx.

cf. *Lacerta vivipara*

Material. THR #327. One right femur, one left ilium, one trunk vertebra and one posterior half of a caudal vertebra. THR #88. One cloacal vertebra. THR #102. One fragmentary trunk vertebra. THR #457. One partial left innominate.

Remarks. THR #327. These elements match CGO 41/1 in size. The ilium has an obtuse ventral margin. THR #88. The cloacal vertebra has a high neural crest and spine. It is considerably larger (centrum length c.2.2mm) than *L. vivipara* (CGO 41/1) and its centrum is more narrowly constricted, somewhat like *P. muralis*. It is of similar size to one or two cloacal vertebrae of *L.*

agilis (CGO 18/1), but is more robust and has a larger articular condyle. The transverse processes have their tips missing. The trunk vertebra is larger, more elongate (possibly from a female specimen?) and more robust than any vertebrae of CGO 41/1. It has a very low crest and the posteriorly directed neural spine is broken. The zygapophyses are very robust. The centrum is broad and only slightly constricted. These elements probably belong to a particularly large *L. vivipara*. THR #457. The partial innominate consists only of the acetabular area with part of the pubis. It is is slightly larger than CGO 41/1.

Anguis fragilis

Material. THR #327. One trunk vertebra, two caudal vertebraa, one posterior half of a caudal vertebra, one fragmentary vertebra, two partial ribs, one partial frontal and five osteoderms. THR #349. One trunk vertebra, one partial trunk vertebra and one osteoderm. THR #531. One osteoderm. THR '89 Yellow clay 13.10.89. One caudal vertebra. THR #530. One partial trunk vertebra, one rib, one right quadrate and twelve osteoderms. THR #537. One osteoderm. THR #538. One trunk vertebra. THR #88. One partial trunk vertebra and one anterior half of a caudal vertebra. THR #398. One osteoderm. THR #102. One caudal vertebra and one partial trunk vertebra. THR #451. One partial trunk vertebra. THR #325. Three ribs and eighteen osteoderms. THR #457. One trunk vertebra and one osteoderm. THR #345. One trunk vertebra and four osteoderms. THR #110. One osteoderm. THR #533. One trunk vertebra and two osteoderms. THR #521. One trunk vertebra, onbe partial trunk vertebra and five osteoderms. THR #520. One trunk vertebra, one partial trunk vertebra and four osteoderms. THR #354. Two trunk vertebrae, one juvenile trunk vertebra, three trunk vertebral fragments, one anterior half of a caudal vertebra, one posterior half of a caudal vertebra, one rib, two partial ribs and fifteen osteoderms. THR #346. One trunk vertebra, one anterior half of a caudal vertebra and one posterior half of a caudal vertebra. THR #351. One trunk vertebra, one caudal vertebra, one posterior half of a caudal vertebra and two osteoderms. THR #535. One partial rib. THR #498/499. One juvenile trunk vertebra. THR #347. Two osteoderms. THR #497. One juvenile posterior half of a caudal vertebra. THR #343. One osteoderm.

Remarks. THR #327. One of the caudal vertebrae is illustrated in Figure 6.21g.

cf. *Anguis fragilis*

Material. THR #74. One partial left ilium.

Remarks. THR #74. This is the first time an *A. fragilis* pelvic element has been recorded fossil from Britain. It is about 30% larger than the corresponding element in specimen CGO 16/4, and is robust with a serrated anterior edge of the corpus.

TORBRYAN SIX CAVE

Torbryan Six Cave (NGR SX816675) is situated close to Tornewton Cave, at a slightly higher elevation, and is probably part of the same system (Roberts, 1996). It is a Scheduled Ancient Monument owing to the Mediaeval chapel built onto the north-facing entrance. Widger conducted excavations in the mid-19th Century and Zeuner carried out further work in 1955-6. Small scale digging was directed by A. Roberts for the BM in 1991. The stratigraphy and faunal finds have not been published, but Figure 6.22b is a schematic representation of the deposits. Much of the sediments are believed to be contemporaneous with sediments at Broken Cavern and Three Holes Cave (Roberts, 1996) and with the Middle Devensian loess of Tornewton Cave (A. Roberts, pers. comm., 1998).

The top of the sequence is capped by a speleotherm deposit, beneath which there is at least 1m of Stony Cave Earth (Roberts, pers. comm., 1998). Within this layer, a lens of Dark Earth has been interpreted as a Late Upper Palaeolithic hearth. AMS dates from this layer are: reindeer tooth, 11,130±100 ^{14}C BP (OxA-3894) and arctic hare thoracic vertebra, 12,130±110 ^{14}C BP (OxA-3895). Beneath the Stony Cave Earth, there is a windblown silt (loess) deposit which is believed by A.P. Currant and S. Collcutt to be linked directly to a similar deposit in Tornewton Cave (Roberts, pers. comm., 1998). An AMS date on horse from this silt gave an age of 32,100±630 ^{14}C BP (OxA-3896).

Two samples produced a few sparse herpetofaunal remains. These are held at the NHM. The only taxa that were recovered are *Rana* sp. and *A. fragilis*, as shown below.

Stony Cave Earth (Lateglacial and Holocene):	TB6 #039	*Rana* sp.
Dark Earth (Lateglacial Interstadial):	TB6 Dark earth	*Rana* sp., *A. fragilis*

Systematic palaeontology

Rana sp. indet.

Material. TB6 #039. One right angulosplenial. TB6 Dark earth. One right angulosplenial.

Remarks. These are probably *R. temporaria*, but cannot be specifically identified

Anguis fragilis

Material. TB6 Dark earth. One osteoderm.

WOOKEY HOLE (HYAENA DEN), nr. WELLS, SOMERSET

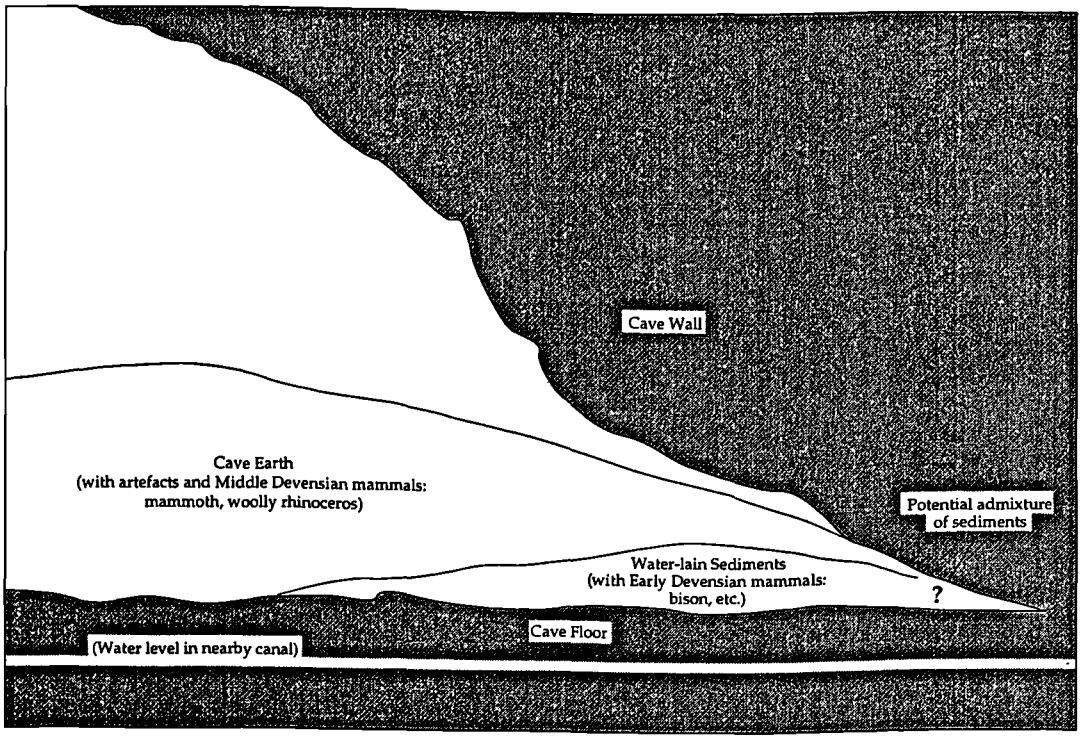
Excavations at the Hyaena Den of Wookey Hole (NGR ST532481) in the Mendip Hills, Somerset, began during the last century (Dawkins, 1863). Numerous vertebrate remains have also been collected during recent excavations. A large amount of excavated material awaits analysis at Wookey Hole Museum and specific stratigraphic descriptions have not been formulated. Basal sediments in the south side of the cave were water-laid, probably when the River Axe was above its present level (R. Jacobi, pers. comm., 1997). These contained an Early Devensian (Banwell-type cf. Currant and Jacobi, 1997) mammal fauna with brown bear, wolf, red fox, reindeer, bison and *Microtus* sp. Overlying these sediments is a cave earth which comprises the main sequence (see Figure 6.23a). It produced artefacts and contained a Coygan-type mammal fauna, i.e. the Hyaena Den, which Currant and Jacobi (1997) attributed firmly to Stage 3. These 'cold continental' assemblages are typical of central Asia today (Currant, pers. comm., 1998) and post -date the 'cool oceanic' Banwell-type faunas, which are relatively impoverished when compared to later Stage 5 faunas of fully temperate character (Currant and Jacobi, 1997). Eight Radiocarbon dates on Coygan-type faunas gave ages between 40-43ka BP. Notably, two of the Coygan-type faunas (from Tattershall and Isleworth) are associated with thermophilous beetle faunas and freshwater Mollusca with affinities to Upton Warren (Jacobi, pers. comm., 1997). Human remains from the Wookey Hyaena Den yielded an AMS date of 40,400±1600 ^{14}C BP (OxA-4782) (Currant and Jacobi, 1997). Another date on a wolf canine gave an age of 39,100±1,300 ^{14}C BP (OxA-5704) and a date on reindeer is awaited (Jacobi, pers. comm., 1997). Though radiocarbon dates of this magnitude lack reliability and are very difficult to interpret (Coope, 1986), correlation of the Wookey Hyaena Den with the Upton Warren Interstadial Complex (UWIC) is inviting.

A series of nineteen samples from the water-lain sediments yielded herpetofaunal remains. The numerous remains are mostly fragmentary and apparently water-rolled, as would be expected from the fluvial nature of the deposits. Owing to the restricted nature of their location, the exact stratigraphic position of these samples is not known. However, by the inclusion of *B. calamita* , it seems probable that at least some of the herpetofaunal material comes from close to the junction between the water-lain sediments and the cave earth. If so, an age at the junction of Stages 3 and 4 seems probable. It is anticipated that additional material, with detailed stratigraphic control, will soon be available (Jacobi, pers. comm., 1998). The herpetofaunal taxa recovered are as follows: *B. calamita, B.* cf. *calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *A. fragilis*. Table 6.6 shows the taxa recovered from each sample.

Table 6.6.

Sample name	*Taxa recovered*
South	*R. temporaria,* Anura indet.
South F	*B. calamita, R. temporaria, Rana* sp., Anura indet.

a)



b)

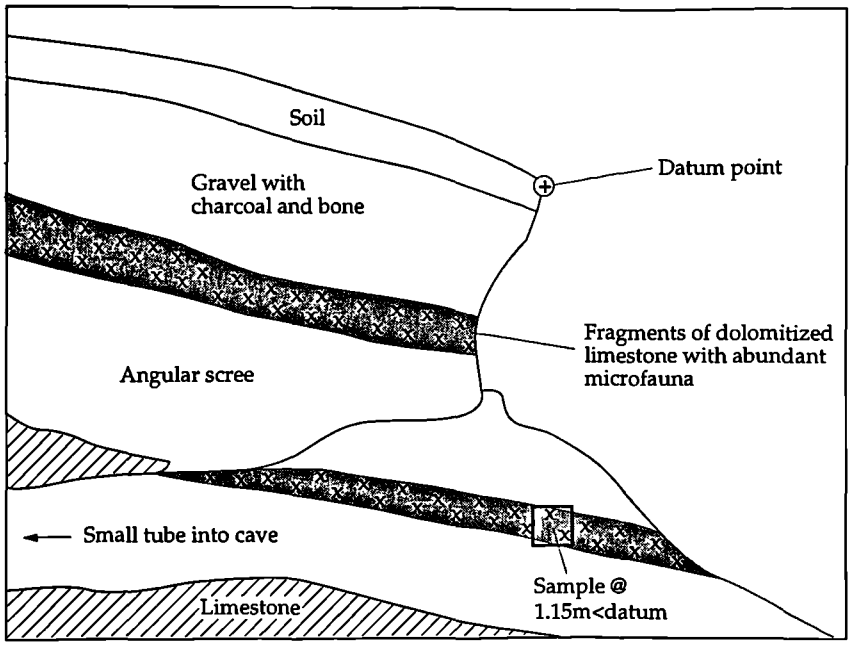


Figure 6.23: a) Schematic representation of the Early and Middle Devensian deposits in the Wookey Hole Hyaena Den, Somerset (modified from A.P. Currant, unpublished); b) Schematic representation of deposits at Denny's Hole, Somerset (modified from A.P. Currant, unpublished).

(S') 4	*R. temporaria, Rana* sp., Anura indet.
(S') 5	*R. temporaria, Rana* sp., Anura indet.
W13	*Bufo* sp., *R. temporaria, Rana* sap., Anura indet., *A. fragilis*
Y13	*R. temporaria, Rana* sp., Anura indet.
HDH 33	*Bufo* sp., Anura indet., *A. fragilis*
I15 ext. 7	*Rana* sp.
H14/I14 C	*B. calamita, R. temporaria, Rana* sp., Anura indet.
H14/I14 (S') B	*R. temporaria, Rana* sp., Anura indet.
H14/I14 (S') D	*R. temporaria, Rana* sp., Anura indet.
HDH(S') H14+I14 A'	*B. calamita, R. temporaria, Rana* sp., Anura indet.
I14/K14/K15 ($) 6f/7 (?)	*R. temporaria, Rana* sp., Anura indet.
(S) I14/I15 ext. 6b	*R. temporaria, Rana* sp., Anura indet.
($) I15 ext. 6b (f?)	*R. temporaria, Rana* sp., Anura indet.
(S) K15 ext. 6b	*R. temporaria, Rana* sp., Anura indet.
(S) I14/K15 ext. 6b	*R. temporaria, Rana* sp., Anura indet.
(S) I15 ext. 6b	*R. temporaria, Rana* sp., Anura indet.
I14 (S) ext. 5	*R. temporaria, Rana* sp., Anura indet.

Systematic palaeontology

Bufo calamita

Material. H14/I14 C. One left ilium. HDH(S') H14+I14 A. One left scapula.

Remarks. These elements are shown in Figure 6.16c.

Bufo cf. *calamita*

Material. Sample South F. One sacrum.

Remarks. These elements are shown in Figure 6.16d.

Bufo sp. indet.

Material. Sample W13. One tibiofibula. HDH 33. One partial tibofibula, one partial femur, one phalanx and one partial trunk vertebra.

Remarks. The tibiofibula (W13), the nutritious foramina are wide, and the shaft is swollen around this area. This may belong to *B. calamita*, but can only be referred to *Bufo* sp. with certainty.

Rana temporaria

Material. Sample HDH(S') H14+I14 A. Three left ilia. (S) I14/I15 ext. 6b. Two left and one right ilium. ($) I15 ext. 6b (f?). One left ilium. (S) K15 ext. 6b. One right ilium and one left

humerus. (S) I14/K15 ext. 6b. One right ilium. (S) I15 ext. 6b. One right ilium. I14 (S) ext. 5. Three left ilia. H14/I14 C. Two left and one right ilium. Y13. One right ilium. H14/I14 (S') D. Two left and three right ilia. (S') 5. Three left and four right ilia. 'South'. Two left and two right ilia. 'South F'. One left ilium. I14/K14/K15 ($) 6f/7 (?). Two left and one right ilium. H14/I14 (S') B. Four left and three right ilia. (S') 4. One right ilium. W13. Two left and one right ilia.

Remarks. The ilia are generally of a consistent form, with three-ribbed tubers, like those from Holocene cave-earths. They are similar to the modern type A forms, and often have fairly high vexillum blades, sloping down from the tuber, deflecting medially and becoming thicker as they become lower.

Rana sp. indet.

Material. Sample HDH(S') H14+I14 A. One left ilium, one femur, one sacrum, one scapula and six radioulnae. (S) I14/I15 ext. 6b. One femur, two radioulnae and one right ilium. ($) I15 ext. 6b (f?). One right ilium, two ilial (ala) fragments, one coracoid, one radioulna, one tibiofibula, one scapula, one male and one female metacarpal II. (S) K15 ext. 6b. One left humeral fragment and one maxillary fragment. (S) I14/K15 ext. 6b. Three scapulae, one humeral fragment, one male metacarpal II, three radioulnae, one sacrum, one femur and two tibiofibulae. I15 ext. 7. One right humeral fragment. (S) I15 ext. 6b. Two left ilia, two scapulae, one left humerus, two maxillary fragments, six radioulnae and a two tibiofibulae. I14 (S) ext. 5. Nine tibiofibulae and femoral fragments, one maxillary fragment and two radioulnae. H14/I14 C. Four femora, one distal phalanx, one ilial (ala) fragment, one maxillary fragment, one sternum and one urostyle. Y13. Three tibiofibulae, one femur, one male metacarpal II, one scapula, two coracoids and one distal phalanx. H14/I14 (S') D. One sacrum and one male metacarpal II. (S') 5. Two distal phalanges, one radioulna, one maxillary fragment, one left and two right humeri. Sample South. Six tibiofibulae, one sacrum, two male metacarpals II, and a maxillary fragment. 'South F'. Two ilial fragments, one sacrum, one scapula, seven tibiofibulae and femoral fragments. I14/K14/K15 ($) 6f/7 (?). One left premaxilla, one distal phalanx, one female metacarpal II, two scapulae (one very pathogenic), three tibiofibula fragments and three femora. H14/I14 (S') B. One distal phalanx, one urostyle, one male metacarpal II, one maxillary fragment and six tibiofibulae and fragments. (S') 4. Two ilial fragments, three maxillary fragments, one male metacarpal II and two femora. W13. One right ilium, one ilial fragment, one right squamosal, two omosternums, seven scapulae, one coracoid, one right frontoparietal (parietal only), one sacrum, three male II metacarpals, one right maxilla and one maxillary fragment, three femora, eight partial tibiofibulae.

Remarks. Again, the material is mainly rolled and worn, often very fragmentary (possibly gnawed), and from juvenile animals in many cases. It has been assumed that no anuran genera, other than *Bufo* and *Rana*, are present. As many of the elements (e.g. humeri, vertebrae, omosternum) are distinguishable as brown frog, all of the material will be referred to this group, in the absence of evidence to the contrary. It seems likely, under the circumstances, that this material

also belong to *R. temporaria*. A fragmentary ilium from sample W13 has a rather slender, narrow tuber and a very thin bladelike vexillum. The specimen is incomplete, but does bear some resemblance to *R. arvalis*.

Indeterminate Anura

Material. Sample HDH(S') H14+I14 A. Twenty-three assorted elements and fragments. (S) I14/I15 ext. 6b. Two trunk vertebrae and eighteen fragments. ($) I15 ext. 6b (f?). Twenty-one elements and fragments. (S) K15 ext. 6b. Nine fragments. (S) I14/K15 ext. 6b. Twenty-seven elements and fragments. (S) I15 ext. 6b. Thirty-eight elements and fragments. I14 (S) ext. 5. Ten fragments. H14/I14 C. Forty-eight elements and fragments. Y13. Twenty-four elements and fragments. H14/I14 (S') D. Forty-one elements and fragments. (S') 5. Fifty-eight elements and fragments. 'South'. Twenty-two elements and fragments. 'South F'. Two vertebrae, one exoccipital and sixteen other elements and fragments. I14/K14/K15 ($) 6f/7 (?). Twenty-five elements and fragments. H14/I14 (S') B. Twenty-one fragments. (S') 4. Twenty fragments. W13. Six humeri, one parasphenoid, four urostyles, two radioulnae, one vertebra, two right angulosplenials, two coracoids, one precoracoid, and ninety-seven other elements and fragments thereof (mainly metacarpals and phalanges). HDH 33. One juvenile humerus, two metapodial fragments, one partial ischium and one partial exoccipital.

Remarks. In some cases, this material could probably be identified to genus though not species. However, most of it is likely to belong to *R. temporaria* and it is unlikely that further scrutiny would be of any additional benefit. The material includes a variety of skeletal elements, but as the material is mainly rolled and fragmentary, some smaller and weaker elements are lacking.

Anguis fragilis

Material. Sample W13. One osteoderm. HDH 33. Two osteoderms.

Remarks. These could be intrusive as they are paler than the other bones in the same samples. However, all of the bones from these samples are less iron-stained than in the other samples.

MILTON HILL CAVE, nr. WELLS, SOMERSET

This is a small cave (NGR ST539471) on Milton Hill in Somerset. It is not to be confused with Milton Hill Fissure which was excavated nearby and yielded hippopotamus (A.P. Currant, pers. comm.). There is no information on the stratigraphy of Milton Hill Cave.

A small sample of sieved 'frog-earth' collected by Currant was studied in 1997. It yielded the following herpetofaunal species: *T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *A. fragilis, N.* cf. *natrix.*

Systematic palaeontology

Triturus vulgaris/helveticus

Material. One trunk vertebra and one caudal vertebra.

Remarks. These vertebrae are small, with a high neural spine, and apparently belong to a smaller newt species. They are in reasonable condition, but have been slightly crushed. Specific identification would not be possible with certainty, but the appearance of the caudal vertebra (in anterior view) is more like *T. helveticus* than *T. vulgaris.*

Bufo bufo

Material. Three left and four right ilia. One left frontoparietal, one right squamosal and one sacrum.

Remarks. The ilia are clearly within the range of *B. bufo.* Their tubers vary in form, from roughened outlines to relatively rounded outlines, but with a sub-cuboid relief on its lateral face.

Bufo sp. indet.

Material. Two left and one right suprascapula. Three scapulae, four radioulnae and five left humeri. One left ilium (ala only). One left maxilla, one right premaxilla, one trunk vertebra and one femur.

Rana temporaria

Material. Two left and three right ilia.

Remarks. The ilia have steep roughened tubers, with varying degrees of lateral sculpture. Some are similar to the type A forms from the Denny's Hole cave earth described above. However, this material is quite worn and possibly rolled.

Rana cf. *arvalis*

Material. One right ilium.

Remarks. See Figure 6.24d. This ilium has its vexillum broken, but the tuber is slender and almost faceted, as in some recent *R. arvalis* studied.

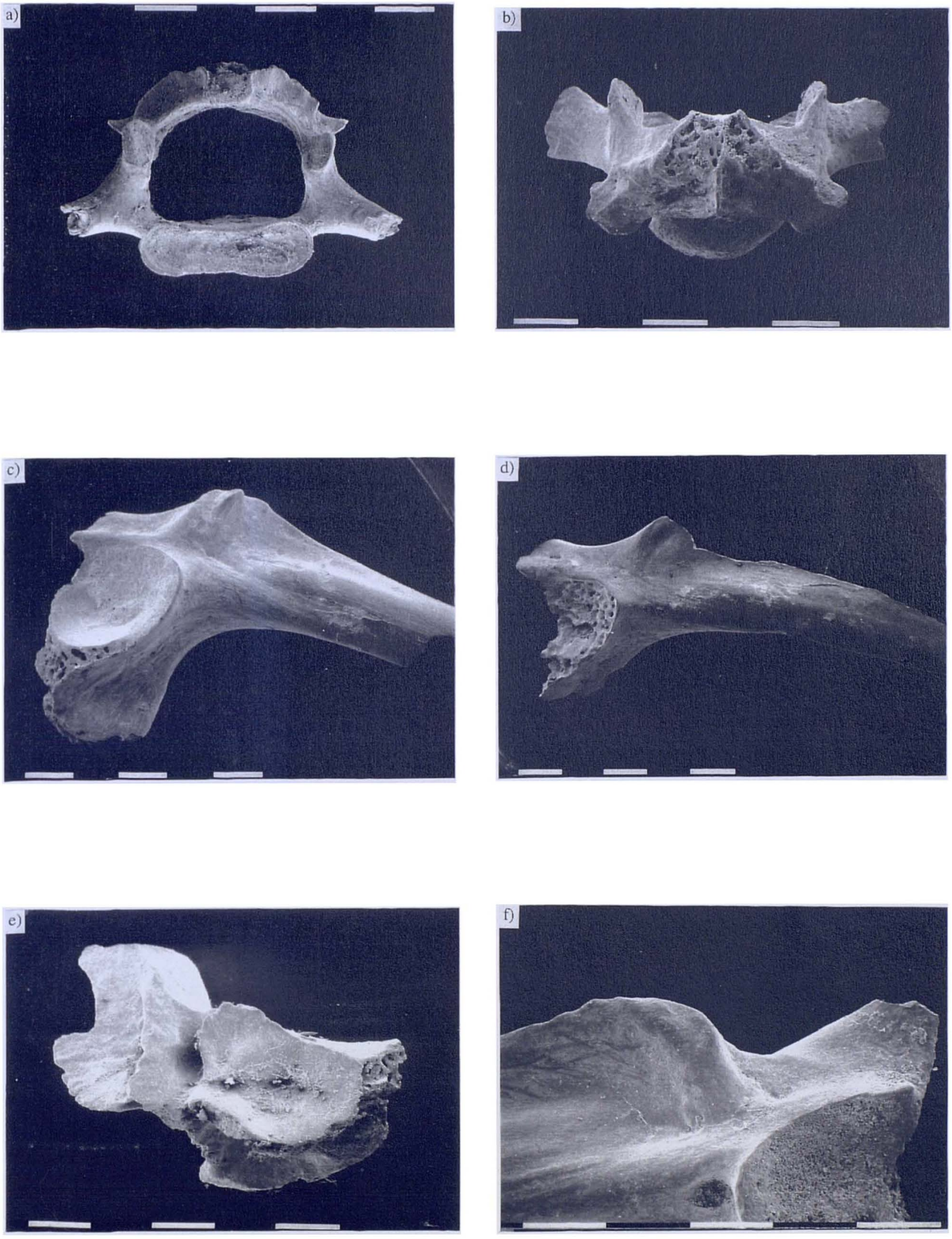


Figure 6.24: Anuran remains from Rogers' Cave (a-b), Milton Hill Cave (c-d), and Denny's Hole (e-f): a) second vertebra of *B. calamita*, anterior view (sample RC 183); b) same specimen, dorsal view; c) right ilium of *R. temporaria*, lateral view; d) right ilium of *Rana* cf. *arvalis* ^, lateral view; e) right frontoparietal of *B. calamita*, dorsal view; f) left ilium of *R. temporaria*, lateral view.

Rana sp. indet.

Material. One radioulna and two scapulae.

Indeterminate Anura

Material. Various elements.

Remarks. This material was seen during scanning of the sample residue, but has not been removed from the sample.

Anguis fragilis

Material. Seven trunk vertebrae, one presacral vertebra, and eleven caudal vertebrae, or parts thereof. Two ribs and twenty-two osteoderms.

Remarks. This material clearly came from at least two animals; one juvenile and one adult.

Natrix cf. *natrix*

Material. Two trunk vertebrae and two trunk vertebral fragments.

Remarks. One vertebra has its posterior neural arch high, and though the hypapophysis has a damaged tip, it is of natricine form. The neural spine is broken. The left prezygapophyseal process shows some pathogenic growth, perhaps relating to a rib breakage or dislocation. As southern European species of *Natrix* would not be expected from Holocene deposits, a tentative referral to *N. natrix* is possible. The second trunk vertebra has a moderately high but straight-sided posterior neural arch, and is probably from the posterior part of the trunk. The neural spine and hypapophysis are broken, but the prezygapophyseal articulations are natricine. The two fragments (partial left and right parts) of one trunk vertebra. The neural arch, neural spine and hypapophysis are missing, but the prezygapophyseal processes are elongate and laterally-directed, cf. *N. natrix* rather than *N. maura/tessellata*.

Indeterminate Ophidia

Material. One trunk vertebral fragment and one juvenile vertebra.

Remarks. The juvenile vertebra is very short, with a large neural canal, and is probably cervical. It has a relatively high neural arch as in *Natrix*, but its elongate hypapophysis has an acute point which might suggest that it belongs to *Vipera*. Diagnosis to genus is not possible.

DENNY'S HOLE, COMPTON BISHOP, SOMERSET

Denny's Hole is a small cave (NGR ST397550) situated on Crooked Peak, in the Mendip parish of Compton Bishop. The only stratigraphic information available is from sketched section drawings (see Figure 6.23b), made by A.P. Currant on a visit in 1982. These very brief notes were kindly provided by Currant (pers. comm., 1997), and as no other work has been published on the cave, no other information is available. Within Denny's Hole, beneath a sharp overhang, a section was cut through a sloping sequence of sediments. The stratigraphy appears to have comprised a layer of 'gravel with charcoal and bone' (c.50-70cm thick), underlain by a discrete layer of 'frog-earth' (c20cm thick) and a thick unit of 'angular scree' continuing downwards below the base of the exposed section. The microfaunally rich layer consisted of dolomitised limestone fragments with abundant rodent and frog bones (Currant, pers. comm., 1997), and from the sketches, appears to have dipped at an angle of 20-30°. Outside the cave, an eroded section shows the same sequence, perched above and around a small tube entering the bedrock (see Figure 6.23b). The top of the sequence was capped with a thin layer of soil, the edge of which Currant used as a datum point. At 1.15m below this, Currant took a small sample of the 'frog-earth'. Small mammals from the sample have not been studied.

The sieved residue of c.100g was examined for herpetofaunal remains. Only anuran remains were observed and the following assemblage was extracted: *B. calamita, R. temporaria, Rana* sp., Anura indet. All specifically diagnostic elements were extracted, but some of the less diagnostic elements have not been removed from the sample. It is particularly notable that, except for the cranial element of *B. calamita* described below, no remains of *Bufo* were observed. The absence of *B. bufo*, and the impoverished nature of this herpetofauna, point quite strongly towards a Lateglacial Interstadial age for this assemblage. It may also be significant that the 'frog-earth' lay beneath a charcoal- and bone-rich layer (Currant, pers. comm., 1997), which could conceivably be a Late Upper Palaeolithic hearth.

Systematic palaeontology

Bufo calamita

Material. One fused right frontoparietal and prootic.

Remarks. See Figure 6.24e. Much of the frontoparietal is missing, but part of the serrated medial edge of the pars parietalis is intact, posteriorly. The linea, or more appropriately, the crista transversalis and crista occipitalis are very strong, and produced into sharp crests. The intervening trough is deep and wide, and is bordered anteriorly by the pronounced crista prooticalis, which is overridden by a flared flange connecting it with the crista occipitalis. The crista parietalis is thickened and leans medially. The frontoparietal and prootic belongs to an animal of c.50-60mm snout-vent length. Of the vertebrae described below, none were apparently of *B. calamita.*

Rana temporaria

Material. Fifteen left and seven right ilia, five left and two male right humeri.

Remarks. All the ilia are of a very similar form. Their tubers are consistently relatively high and steep, laterally bulbous, often with three diverging ribs. Their vexillums are fairly continuous. Notably, all the ilia have a deep pre-acetabular fossa (see Figure 6.24f). The humeri are of males and have wide and continuous, posteriorly directed cristata cf. *R. temporaria.*

Rana sp. indet.

Material. Twenty-four trunk vertebrae, six sacra, one dentary, three radioulnae, two left and one right humeri, one left and one right frontoparietal, fifteen scapulae, ten coracoids, nine femora, fourteen tibiofibulae and various fragments.

Remarks. The vertebrae show some variability, but generally have a strong, but well-rounded transverse dorsal crest. On one specimen, this is somewhat posteriorly-deflected, with a small nodular posterior process evident. Another has particularly small articular facets. All this material probably also belongs to *R. temporaria.*

Indeterminate Anura

Material. Various elements constituting most of the skeleton.

LOWER CAVE, CLIFTON, BRISTOL, AVON

This cave (NGR ST566732) is situated at the base of the cliff, below the observatory at Clifton, adjacent to the Clifton Suspension Bridge. It is located on the east bank of the tidal reaches of the River Avon, about 5km before it reaches the Severn estuary. It has no published excavational history, but recent small-scale sampling and dating was carried out by A. Baker (University of Exeter). Sediments at the back of the cave are less than 5m above the present high tide limit (Baker, pers. comm., 1998). The base of a flowstone deposit was U-Th dated to 6,000±1,000 years BP, and its top is still actively forming. Sediments below this flowstone were observed to contain small vertebrate remains and are probably of Lateglacial or early Holocene age.

A small sample of the material beneath the flowstone was provided by A. Baker. Very few herpetofaunal remains were identifiable from it. The bones are extensively altered chemically, and are stalagmite-encrusted. They also appear to be trampled or crushed. They are very brittle, whitish in colour and have a chalky crystalline structure The herpetofaunal remains identified are as follows: *R.* cf. *temporaria, Rana* sp., Anura indet.

Systematic palaeontology

Rana cf. *temporaria*

Material. One left frontoparietal and one left humerus.

Remarks. These elements are the only ones complete enough for tentative specific identification.

Rana sp. indet.

Material. Three partial radioulnae, five distal phalanges and one ilial (ala) fragment.

Remarks. The radioulnae have their olecranons more produced than in *Bufo*. The phalanges are slender. The ilial fragment includes part of the vexillum, and probably belongs to *R. temporaria.*

Indeterminate Anura

Material. Three partial radioulnae, one humeral fragment, one sphenethmoid, one partial right angulosplenial, two vertebral fragments, one distal phalanx and seventeen other fragments and phalanges.

Remarks. These are too fragmentary or damaged to allow identification to genus, though they are probably *R. temporaria* also.

WYE VALLEY CAVES, HEREFORDSHIRE AND GWENT

Several caves in a tightly meandering section of the River Wye gorge, in the Symonds Yat area, have been investigated since 1993 by N. Barton (Oxford Brookes University). The area has a high density of caves and rockshelters (c.40), with deposits spanning the Devensian Lateglacial and most of the Holocene (Barton *et al*, 1995). Material from Rogers' Cave (one of the Symonds Yat East Caves, *sensu* Barton, 1994) and Madawg Rockshelter has so far been examined for herpetofaunal remains (see Figure 6.25). Rogers' Cave is situated on the English side of the river in Herefordshire. Madawg Rockshelter is situated on the Welsh side of the river in Gwent, and will be dealt with in the proceeding section on Wales (Chapter 6.2). Preliminary accounts of the lithostratigraphy and archaeology of Rogers' Cave and Madawg Rockshelter were given by Barton (1993; 1994) and Barton *et al* (1997). Formal faunal descriptions are as yet unpublished. The amphibian and reptile remains are described in the following accounts.

ROGERS' CAVE

Rogers' Cave (NGR SO56141550) is also known as Symonds Yat East Cave, No.14 (Barton, 1994). It is located in a rockface high above the southeast bank of the River Wye, close to a prominent rock pinnacle known as the Longstone (or locally as 'Peartree Rock'). The cave has a north-facing entrance about 4m wide. Several caves were investigated in the vicinity, but Rogers' Cave was the only one to produce evidence of prehistoric activity (Barton, 1994). Much of the work on this site is not yet published and as yet there are no dates from any of the sedimentary units.

Two areas were excavated in Rogers' Cave during 1994 (Figure 6.26a). Figure 6.26b shows the stratigraphy revealed in Test Area 1. Layers 1-4 are situated at the back of the cave, with Layer 5 being continuous with Layer 4 at the front of the cave. The bulk of the sequence comprises a reddish brown clay with many boulders, large cobbles and gravel. This material is divided into Layer 4, a reddish brown silty clay c.15-60cm thick, and Layer 3, a reddish brown gritty clay c.40 -60cm thick. Layer 4 produced what N. Barton (pers. comm., 1998) has described as an assemblage of 'very typologically clean' and unambiguously Final Upper Palaeolithic artefacts. He places the upper boundary of this period at somewhere between 12-11ka BP, i.e in the Lateglacial Interstadial. Charcoal, possibly of *Corylus*, was also identified from Layer 4. Layer 5 is a lateral equivalent and presumably spans the same period. A cold-climate small mammal fauna was recovered from Layer 3, including collared lemming, Norway lemming and northern vole (C. Price, pers. comm.). Large angular boulders of limestone lie flat with their bases at the junction between Layers 3 and 4, on what was obviously a land surface. The matrix of Layer 3 has filled around these boulders and covers them to a large degree. Since the underlying material from Layer 4 is dated archaeologically to the Lateglacial Interstadial, and the surrounding matrix yielded an arctic small mammal fauna, it is very probable that these boulders are the result of frost shattering during the Lateglacial Stadial. An analogous layer is also present at the nearby King Arthur's Cave,

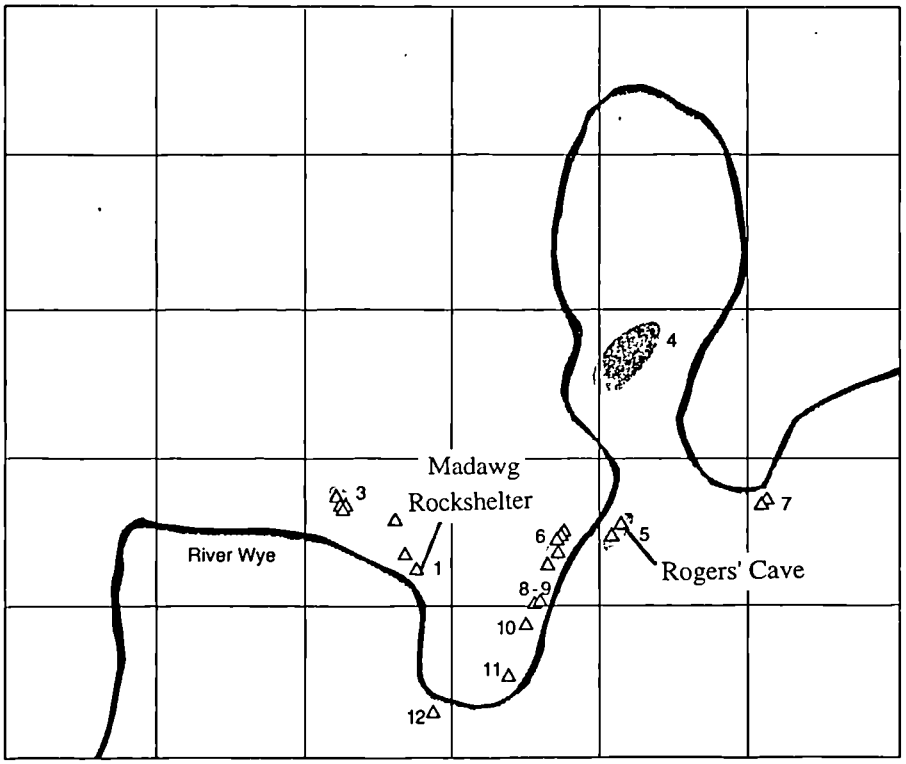
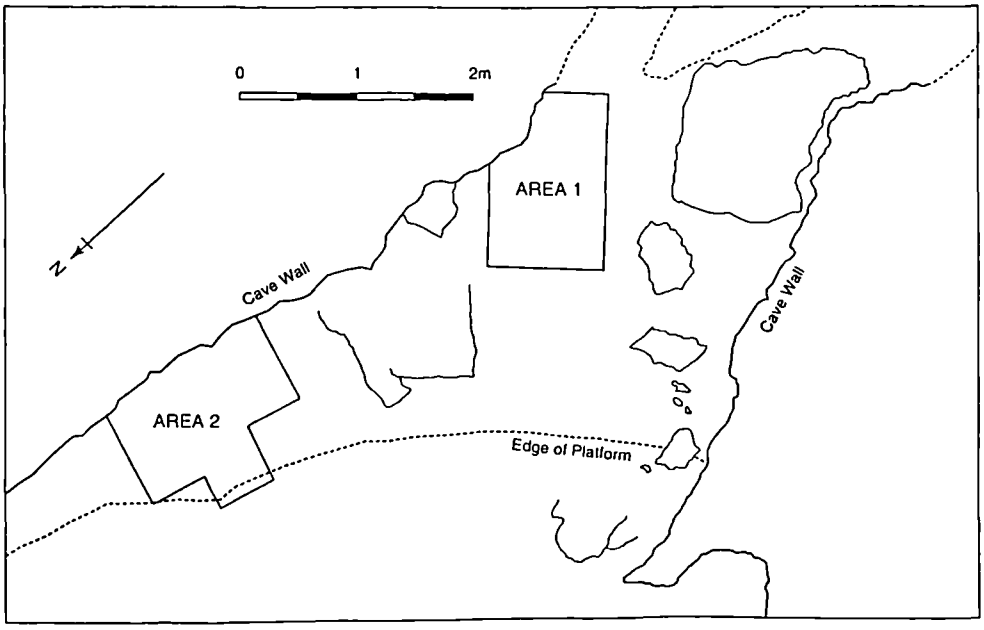
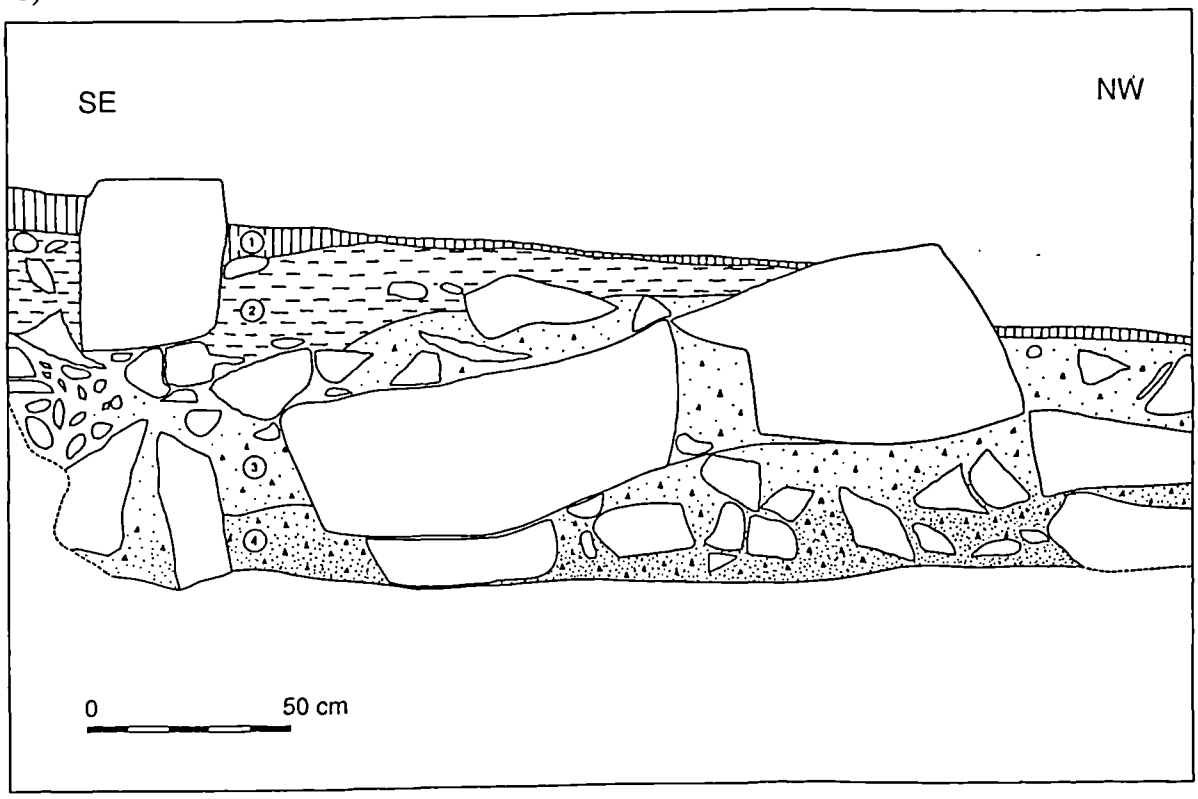


Figure 6.25: Location of the Wye Valley Caves, Herefordshire and Gwent (after Barton *et al*, 1997).

a)



b)



Key: (1) Dark grey-black soil; (2) Tufaceous stalagmite; (3) Reddish-brown gritty clay; (4) Reddish-brown silty clay

Figure 6.26 Rogers' Cave, Herefordshire: a) Plan of cave and excavated areas; b) Lithostratigraphic section of Lateglacial and Holocene deposits in Area 1 (after Barton, 1994).

with an associated fauna including reindeer, arctic hare and the same rodents as above (Roberts *et al*, 1997). Layer 2 is a horizontal swathe of fairly pure tufaceous stalagmite from 10-40cm thick, with only occasional cobbles and gravel. By analogy with apparently widespread tufa formation in other caves in southern Britain (e.g. see sections on Three Holes Cave, Kent's Cavern and Lower Cave), and in various terrestrial areas of southern Britain (e.g. Kerney *et al*, 1980; Preece, 1979), this layer can probably also be assigned an early to middle Holocene age. The sequence is capped by a thin layer of dark grey-black soil, up to 10cm thick.

Herpetofaunal remains were retrieved from sixteen samples of the five contexts. The following herpetofaunal taxa were recovered: *T. vulgaris/helveticus, B. bufo, B. calamita, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis*. Table 6.7 shows the species occurrences within each sample and context.

Table 6.7

Layer 1 (late Holocene?)	
RC #392:	Anura indet., *A. fragilis*
RC #394:	*B. bufo, Bufo* sp.
Layer 2 (early to middle Holocene?)	
RC #2:	*B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *A. fragilis*
RC #17:	*Bufo* sp.
RC #18:	Anura indet.
Layer 3 (Lateglacial Stadial and/or early Holocene?)	
RC #133:	*Bufo* sp., *Rana* sp., Anura indet., *A. fragilis*
Layer 4 (Final Upper Palaeolithic, c.12-11ka BP - Lateglacial Interstadial)	
RC #135:	*B. bufo, Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara*
RC #136:	*B. bufo Bufo* sp., *Rana* sp., Anura indet.
RC #149:	*Bufo* sp., *Rana* sp., Anura indet., *A. fragilis*
RC #159:	*B. bufo, Bufo* sp., cf. *L. vivipara*
RC #165:	*Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara*
RC #183:	*B. calamita, Rana* sp., Anura indet.
RC #400:	cf. *L. vivipara*
Layer 5 (Lateglacial Interstadial)	
RC #268:	*B. bufo, Bufo* sp., *Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis*

Systematic palaeontology

Triturus vulgaris/helveticus

Material. RC #381. One trunk vertebra.

Remarks. RC #381. The vertebra has a low neural spine with a wide, shouldered apex. It is fairly certainly *T. vulgaris*, but *T. helveticus* can be variable within the range of this specimen.

Bufo calamita

Material. Sample RC #183. One second vertebra.

Remarks. The second vertebra is compact, with short transverse processes, and has a very elongate, elliptical anterior cotyle. See Figure 6.24a,b.

Bufo bufo

Material. RC #135/136/159/268 (bones mixed accidentally). One right ilium and one third vertebra. RC #18. One partial sacrum, one right and one partial left frontoparietal. RC #20. One left frontoparietal, one partial sacrum, two radioulnae and one sphenethmoid. RC #381. One left ilium. RC #394. One left and one right scapula. RC #2. Five left and four right ilia, one left and one right juvenile ilia, one sacrum, one partial sacrum, three tibiofibulae, one left and one right frontoparietal, one partial frontoparietal, one right scapula and one partial scapula.

Bufo sp. indet.

Material. RC #135/136/149/159/165/268 (bones mixed accidentally). Two partial tibiofibulae, two radioulnae, two trunk vertebrae, one partial trunk vertebra, one left and two right humeri, two right humeral fragments, one left scapula, one metacarpal and one partial squamosal. RC #18. One partial right ilium, one left and one large right angulosplenial, one femur, one femoral fragment, one fibulare, two metapodials, one phalanx and one left premaxilla. RC #20. One partial left ilium, one right humerus, one metatarsal, one phalanx, one male metacarpal II, three trunk vertebra, one partial atlas, one partial left scapula and one ilial ala. RC #17. One partial tibiale. RC #394. One femur. RC #133. One partial right humerus, one trunk vertebra and one metapodial. RC #2. One partial ilium, eight femora, one partial femur, seven tibiofibulae and fragments thereof, two right male humeri, one left and one right female humerus, one partial left humerus, one right humeral fragment, seven radioulnae, two partial left and one left squamosal, one tibiale, three fibulare, one partial fibulare, one right ilial ala, two left angulosplenials, one male metacarpal II, five partial and two trunk vertebrae, one left suprascapula, three right premaxillae, one phalanx, two partial maxillae, one partial atlas, thirty-seven metapodials and phalanges, two coracoids and one distal phalanx.

Rana temporaria

Material. RC #18. One left ilium. RC #2. One left ilium (juvenile).

Remarks. The ilium has a bulbous tuber cf. recent *R. temporaria.*

Rana sp. indet. (brown frog)

Material. RC #135/136/149/159/165/268 (bones mixed accidentally). One incomplete left humerus. RC #18. One male metacarpal II and one right humerus.

Remarks. The humeri have a strong, posteriorly directed medial crista. The lateral crista is not directed backwards, similar to *R. arvalis*, but is within the range of *R. temporaria.*

Rana sp. indet.

Material. RC #135/136/149/159/165/268 (bones mixed accidentally). One partial maxilla (juvenile), one left and two right scapulae, one trunk vertebra, one sacrum, two fibulare, one metacarpal and one phalanx. RC #18. One precoracoid and one metatarsal (juvenile). RC #20. One femur, one metatarsal and one tibiale. RC #183. Two trunk vertebrae. RC #133. One sacrum and one right angulosplenial. RC #2. One trunk vertebra and one distal phalanx.

Indeterminate Anura

Material. RC #135/136/149/159/165/268 (bones mixed accidentally). Seven partial or fragmentary trunk vertebrae, three urstyles, one metacarpal, three phalanges and one partial frontoparietal. RC #18. One partial female left humerus, two urostyles, one precoracoid, six vertebral fragments, one phalanx, one prootic and one nasal. RC #20. One right squamosal, two radioulnae, one left exoccipital, one ilial corpus fragment, thirteen phalanges, one omosternum, one trunk vertebra, one right pterygoid, one partial left ilium and thirteen fragments. RC #381. Two partial metapodials or phalanges. RC #17. One partial trunk vertebra and one partial phalanx. RC #392. One cranial fragment? RC #183. Two vertebral fragments and a phalanx. RC #133. One partial hyoidal cornu, one ischium, one partial vertebra, one partial squamosal and one partial left humerus. RC #135. One vertebral fragment and four phalanges. RC #2. Three urostyles, four ischia, three humeral fragments, one trunk vertebra and sixty-seven vertebral fragments, three partial coracoids, one partial parasphenoid, one humerus, one carpal, five quadratojugals, four dentaries, five partial angulosplenials, five pterygoids, three precoracoids, three hyoidal cornua, one nasal, one prootic, one squamosal, one radioulna and seventy-nine other elements and fragments thereof.

cf. *Lacerta vivipara*

Material. RC #159/165 (bones mixed accidentally). Three trunk vertebrae. RC #135. One distal right humerus. RC #159. One partial right innominate. RC #165. One incomplete left

innominate and one distal left femur. RC #268. One left femur. RC #400. One posterior half of a posterior trunk vertebra, one partial left scapulocoracoid (scapula portion) and one undeterminate appendicular element (metapodial?).

Remarks. RC #159/165. One of the trunk vertebrae appears too large for *L. vivipara*, but it does not have a sharp crest as in *L. agilis*. It is also very elongate, more so than any of the species studied. This may be due to sexual dimorphism: females have not been studied but may have longer trunk vertebrae. RC #135. The humerus is slightly larger than CGO 41/1 but has no epiphysis. RC #165 and RC #268. Both the femora have fused epiphyses and are thus from mature animals. They are identical in size to specimen CGO 41/1. RC #159 and RC #165. The angle between the ilium and the pubis of the innominates is wide, cf. *L. vivipara*. Both specimens are slightly larger and more robust than CGO 41/1. RC #400. The vertebra and scapula are the same size as CGO 41/1. The undeterminate element is apparently broader than metapodials of CGO 41/1, and bears some resemblance to a humerus in which case it would be a juvenile. This is unlikely as the epiphyses are fused.

Anguis fragilis

Material. RC #149/268 (bones mixed accidentally). One sacrum, one posterior half of a posterior caudal vertebra and three osteoderms. RC #18. Six osteoderms, one anterior half and one posterior half of a caudal vertebra. RC #20. One partial trunk vertebra and fourteen osteoderms. RC #392. One partial trunk vertebra. RC #133. One trunk vertebra and one osteoderm. RC #135. Twenty-two osteoderms. RC #2. Two trunk vertebrae, one partial trunk vertebra, one right frontal, two partial ribs and ninety-one osteoderms.

6.3 Wales

MADAWG ROCKSHELTER, WYE VALLEY, GWENT

This site (NGR SO54651526) is a large west-facing limestone rockshelter, overlooking the River Wye. It lies c.350m south-southeast of King Arthur's Cave, on the north side of a prominent Lower Crease Limestone bluff (part of the Seven Sisters rocks). Its location is shown in Figure 6.25 in the previous section. A plan of the shelter and excavation areas is shown in Figure 6.27a. Sediments beneath the overhang were investigated by the BM between 1993 and 1995, under the direction of N. Barton, and revealed a sequence containing Later Mesolithic and Early Bronze Age artefacts (Barton, 1994; Barton *et al*, 1997). Some early investigations by Hewer in the 1920s, and recent work, is described by Barton *et al* (1997).

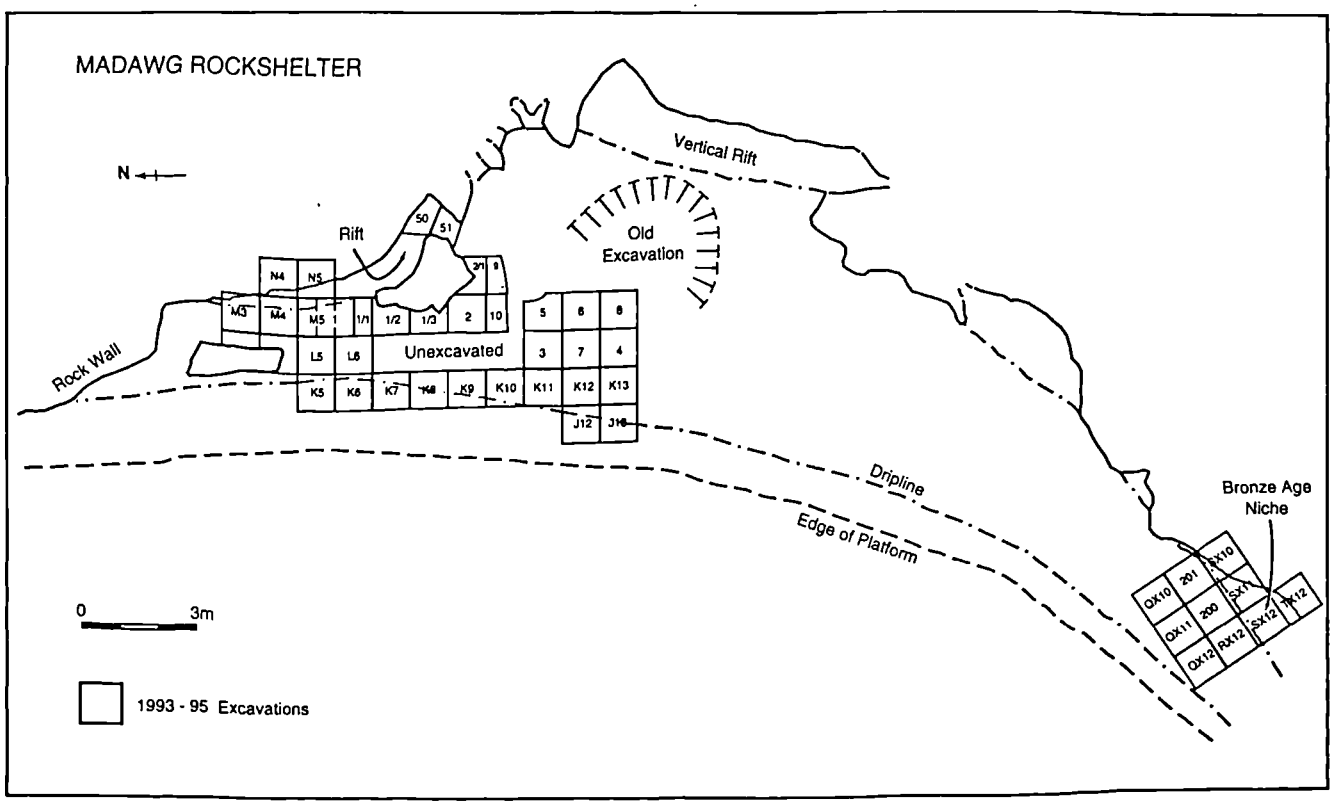
The stratigraphy exposed in an excavated trench is shown is Figure 6.27b. The lowest 50-100cm of sediment are a light brown Stony Cave Earth, containing numerous limestone clasts (Barton *et al*, 1997). A charcoal-rich layer in the southern part of the trench extends to a depth of about 30cm within the Stony Cave Earth. It has been interpreted as a hearth, although magnetic susceptibility is unsupportive of this conclusion (Barton *et al*, 1997). The most remarkable archaeological find is a cluster of eleven perforated European cowrie (*Trivia monacha*) shells which were probably strung together as a necklace (Barton, 1994). Mesolithic microliths and hazelnut shells were also recovered from this unit. Charcoal from the lower levels was identified as pine and yew, with oak, ash and elder higher up. Two AMS dates of 8,710±70 ^{14}C BP (OxA-6081) on a charred sloe stone and 6,655±65 ^{14}C BP (OxA-6082) on a charred hazelnut shell may indicate two separate Late Mesolithic occupations (Barton *et al*, 1997). Overlying the Stony Cave Earth is a Grey Tufaceous Earth, with Middle Bronze Age archaeology, and a Cemented Stalagmite layer. Early Bronze Age sediments were present at the southern end of the shelter, filling a niche in the bedrock where human bones and 'Food Vessel' fragments probably indicate a burial (Barton, 1994). At the northern end of the trench, the Stony Cave Earth is overlain by a Loose Grey Silty Earth. An adjacent overhang, Cavell Shelter, is included here with Madawg Shelter for ease of description. Its deposits comprise a Roman occupation layer about 30cm thick, underlain by a mottled grey (possibly Bronze Age) layer.

Four samples from Madawg and Cavell produced a few very fragmentary herpetofaunal remains of: *Bufo* sp., Anura indet., *A. fragilis*. The taxa recovered from each context and sample are listed in Table 6.8 below.

Table 6.8

Loose Brown Earth (Roman? - late Holocene)
CAVELL #5: *A. fragilis*

a)



b)

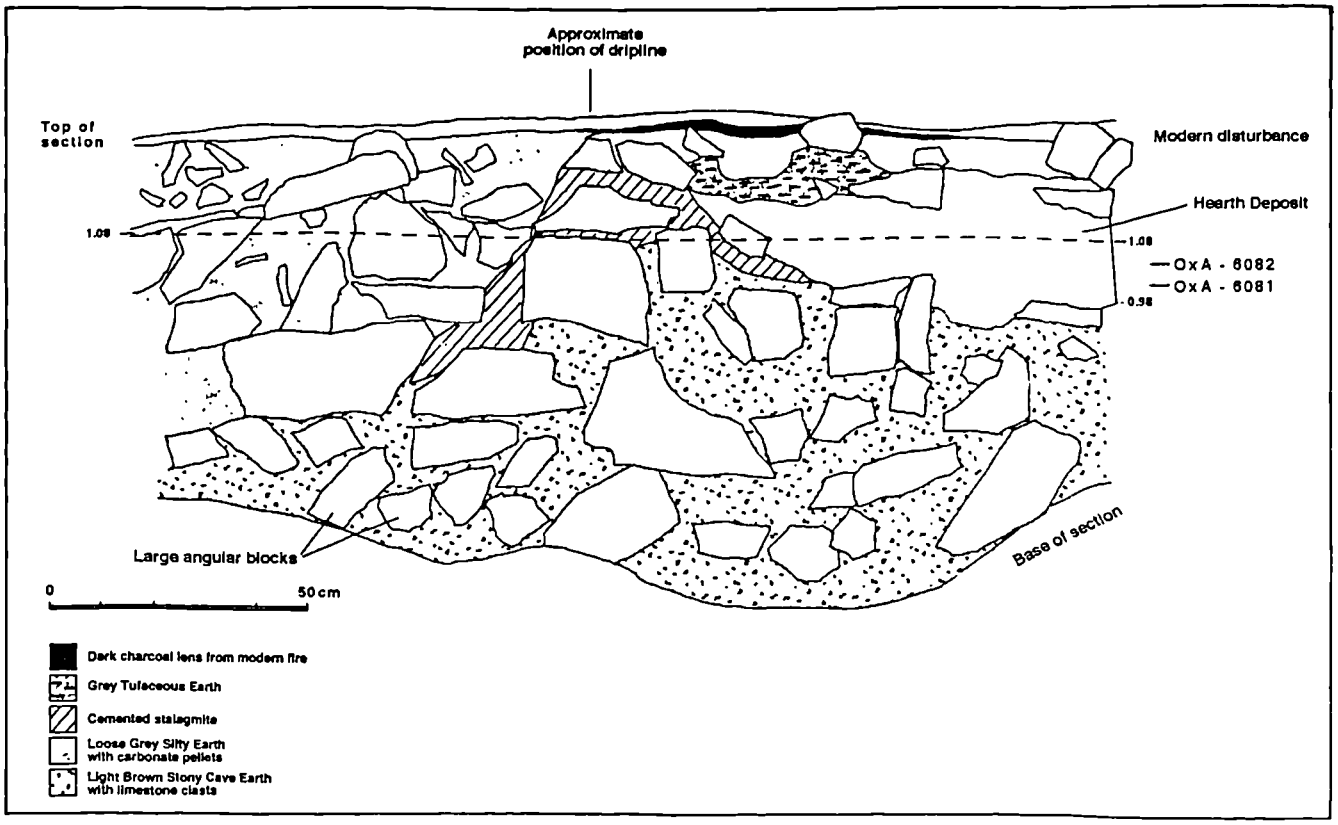


Figure 6.27: Madawg Rockshelter, Gwent: a) Plan of shelter and excavated areas; b) Lithostratigraphic section of Holocene deposits (after Roberts *et al*, 1997).

GTE: Grey Tufaceous Earth (Middle Bronze Age, c.3-3.5ka BP - middle to late Holocene)
MDG #410: *Bufo* sp.

DB2: Stony Cave Earth (Later Mesolithic, ^{14}C dates c.6.6-8.7ka BP - early to middle Holocene)
MDG #418: *A. fragilis*
MDG #528: Anura indet.

Systematic palaeontology

Bufo sp. indet.

Material. MDG #410. One phalanx.

Indeterminate Anura

Material. MDG #528. One partial trunk vertebra.

Anguis fragilis

Material. CAVELL #5. One anterior half of a caudal vertebra. MDG #418. One osteoderm.

HOYLE'S MOUTH CAVE, nr. TENBY, DYFED

Hoyle's Mouth Cave, also known as 'The Hoyle', is a sinuous passage formed in Carboniferous Limestone. Its large entrance opens at 21m above OD (NGR SS112003) into the Ritec Valley near Tenby (Campbell and Bowen, 1989). Various investigations were made during the nineteenth century, including work by Dawkins, and in 1968 systematic excavations were made by Savory. An account of previous work and findings was given by Campbell and Bowen (1989). More recent excavations were carried out by the NMW in 1990 and 1996, under the direction of S.H. Aldhouse-Green. The results are as yet unpublished. Overall, the deposits in the cave have been greatly disturbed, but it appears that there was once a continuous brecciated cave earth up to 1m thick, sealed by a thin layer of stalagmite (Campbell and Bowen, 1989). Savory (1973) described the stratigraphic sequence near the cave entrance as:

4	Disturbed layer with Creswellian flints, Early Iron Age, Roman and post-Mediaeval potsherds, recent animal bones, shells, iron-slag, charcoal and several hearths
3	Powdery yellow earth with bones of hyaena, cave bear and ?bison, and occasional flints
2	Sandy yellow silt
1	Sticky brown earth with stones

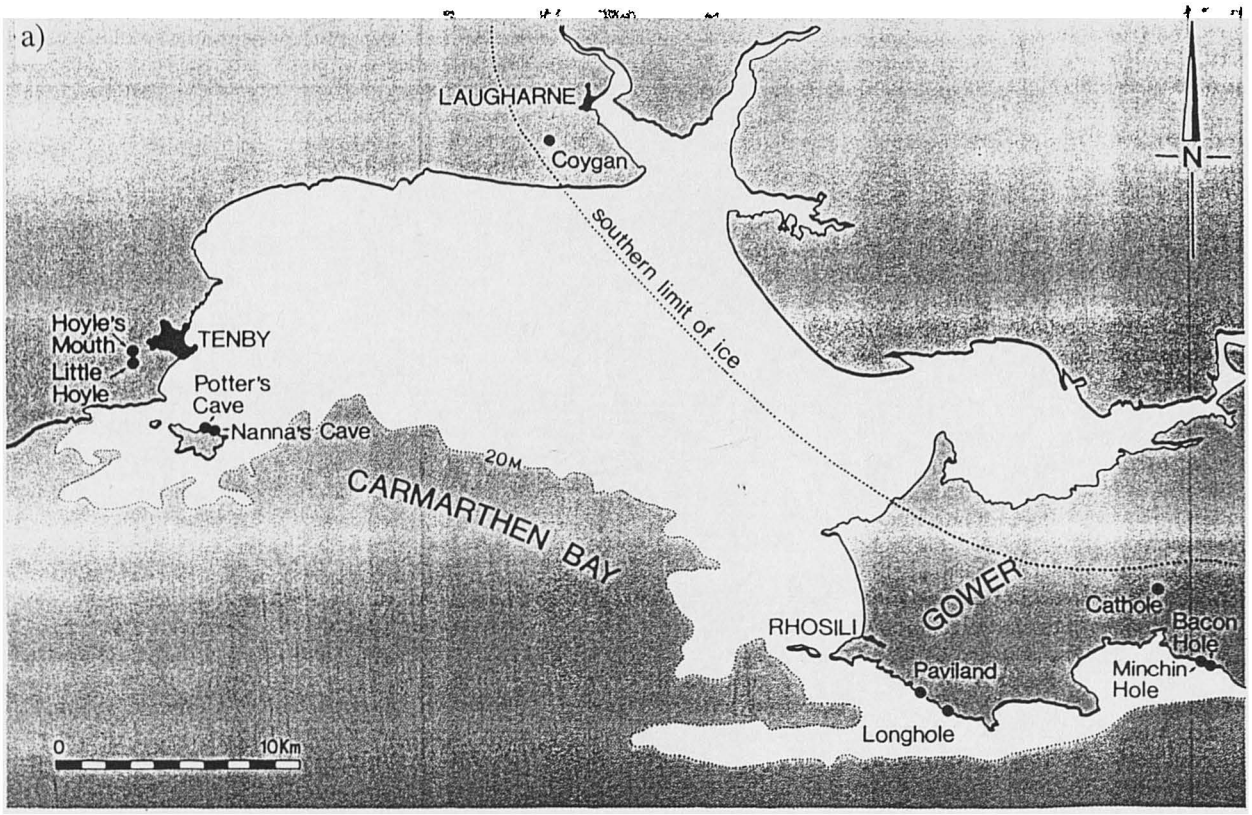
Green and Walker (1991) presented the following stratigraphy:

Stalagmite
Wall sediment
- 1) Trample
- 2) Disturbed soil
- 3A) Yellowish silt (loess)
- 3) Orange silty clay

Bedrock

A stratigraphic scheme for two trenches (Trenches 3 and 5) was supplied by Elizabeth Walker (pers. comm., 1996). This is used in table 6.9 below.

The majority of the archaeological assemblage from Hoyle's Mouth is typical Late Upper Palaeolithic, dating to c.12,500 BP (Green and Walker, 1991). However, an Aurignacian busked burin was also found in the cave and demonstrates an earlier presence at around 30,000 BP (Green and Walker, 1991). Unit 3A of Green and Walker (1991) (cf. Unit 3 Savory, 1973) is a loess sequence, and has been TL dated to between c.23-10kA BP (S.H. Aldhouse-Green, pers. comm., 1996). It yielded bear, fox, reindeer, arctic hare and lemming, and a radiocarbon date on indeterminate bone gave an age of 27,900±600 ^{14}C years BP (OxA-1024) (Green and Walker,



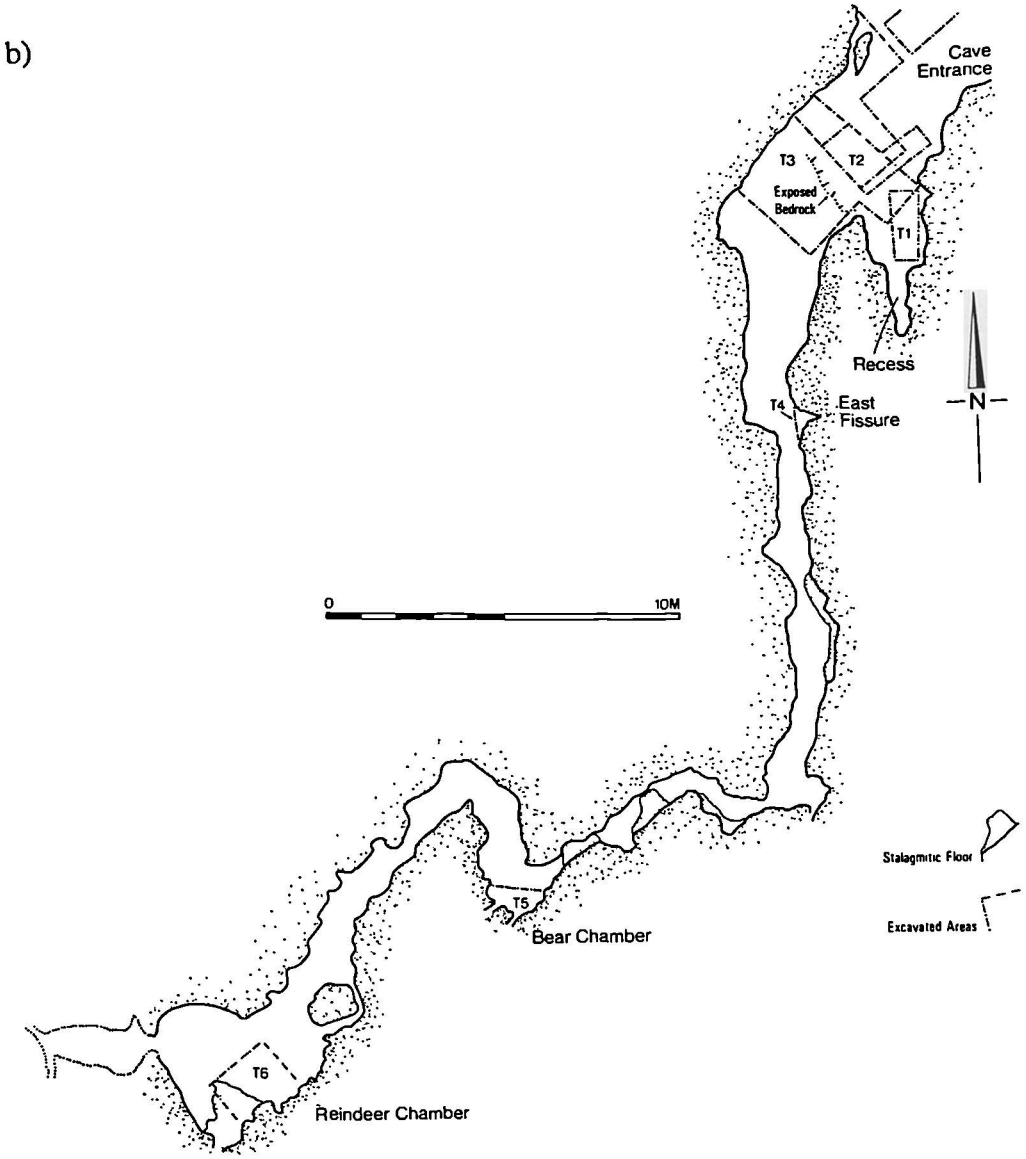


Figure 6.23: a) Location of the South Wales caves (after Green and Walker, 1991); b) Survey of Hoyle's Mouth Cave, Dyfed (after Green and Walker, 1991).

1991). The records of hyaena and bison (Savory, 1973) suggest a Middle Devensian age, but the TL dates imply that loess was only forming close to and after the last glacial maximum. Horse and deer can also be added to the faunal list, though these were recovered (along with bear, hyaena and artefacts) from an 'almost black' soil up to 1m thick by Smith in the 1860's, when disturbance meant their context was uncertain (Green and Walker, 1991).

Small vertebrate remains from the site were studied during a visit to the NMW in 1996. The bones are from the loess sequence and are believed to date to the Devensian Lateglacial Interstadial (c. 13-11,000 BP) (S.H. Aldhouse-Green, pers. comm., 1996), thus it is assumed that they are from the upper part of the loess sequence. The faunal remains had been sieved using a 1mm mesh, then picked by A.P. Currant and accessioned separately. Virtually all of the herpetofaunal material consisted of anuran ilia, often in very good condition, with a few other bones such as scapulae and tibiofibulae. No newt or reptile bones were seen. The herpetofaunal material is now labelled with original sample names and sub-bagged within the original bags, and held at the NMW. The following taxa were identified: *B. bufo, B. calamita, Bufo* sp., *R. temporaria*. The taxa recovered from each sample are listed in Table 6.9.

Table 6.9.

Trench 3		
Layer 2	#882	*B. bufo*
Layer 5	#1113	*B. calamita*
	#1575	*B. calamita*
Trench 5		
Layer 1	#922	*B. bufo*
	#995	*R. temporaria*
	#1021	*R. temporaria*
	#1024	*B. bufo*
	#1025	*B. bufo*
	#1032	*B. bufo*
	#1485	*R. temporaria*
Layer 2	#1016	*R. temporaria*
	#1169	*R. temporaria*
	#1173	*B. bufo*
	#1178	*B. bufo*

	#1187	*R. temporaria*
	#1190	*R. temporaria*
	#1191	*B. bufo*
	#1192	*B. bufo*
	#1366	*R. temporaria*
	#1546	*B. bufo*
	#1775	*R. temporaria*
	#1778	*B. bufo*
Layer 3	#1713	*Bufo* sp.
	#1721	*B. bufo*
	#1741	*B. bufo*
	#1742	*B. bufo*
Layer 4	#1595	*R. temporaria*
	#2122	*B. bufo*
	#2131	*R. temporaria*
Layer 5	#1457	*B. bufo*
	#1468	*B. bufo*
Layer 5c	#1606	*B. bufo*
	#1611	*B. bufo*
	#1625	*B. bufo*
	#1627	*R. temporaria*
	#1650	*B. bufo*
	#1651	*B. bufo*
	#1671	*B. bufo*
	#1674	*B. bufo*
	#1682	*B. bufo*
Layer 5d	#1877	*B. bufo*
	#1885	*B. bufo*
	#1895	*R. temporaria*
	#2015	*R. temporaria*
	#2043	*B. bufo*
	#2051	*R. temporaria*
Layer 5e	#2069	*R. temporaria*
Layer 5g	#2399	*B. bufo*

(Context not known, probably also Lateglacial)

#195	*R. temporaria*
#206	*R. temporaria*
#219	*B. bufo*, *Rana* sp.
#306	*R. temporaria*
#309	*B. bufo*
#371	*B. bufo*
#1402	*R. temporaria*
#1689	*B. bufo*
#1707	*B. bufo*
#2569	*R. temporaria*
#2579	*R. temporaria*
#2682	*B. bufo*
#2762	*R. temporaria*

Systematic palaeontology

Bufo bufo

Material. Sample HM90 T3 (5) #1025. One right ilium. #1032. One right ilium. #1024. One left ilium. #922. One left ilium. #922. One left ilium. #1707. One sacrum. #1721. One right ilium. #1742. One left ilium. #1741. One left ilium. #2122. One left ilium (juvenile). #1191. One right ilium. #1778. One right ilium. #2178. One left ilium. #1173. One left ilium (juvenile). #1546. One right scapula. #1192. One left ilium. #882. One right ilium. #1457. One left ilium. ##2043. One left ilium. #2399. One right ilium. #1877. One right ilium. #1885. One left ilium. #1674. One left ilium. #1625. One left ilium. #1682. One left ilium. #1671. One left ilium. #1606. One left ilium. #1689. One right ilium. #1611. One left ilium. #1650. One left ilium. #1651. One right ilium. #1468. One right ilium. #309. One right ilium. #371. One right ilium. HM96 #2682. One left ilium. #219 (presence noted, not exhaustively studied).

Remarks. The ilia are all clearly within the morphological range of *B. bufo*, and easily separable from *B. calamita*. #1032 has a ridge-like tuber. #1742 has a deeply-undercut pars descendens, but not as deep as in *B. viridis*. #2178 has a very strong ventrolateral ridge along its ala. #1885 and #1682 have fairly angular tubers, but are still within the range of *B. bufo*. #1778 is only a partial specimen and is pathogenic.

Bufo calamita

Material. Sample HM90 T3 (5) #1113. One right ilium. #1575. One right ilium.

Remarks. #1113 has a very steep, sharply pointed tuber, like the Ightham specimens. Ala

has a fairly strong ridge, but not a 'blade'. Pars descendens damaged. #1575 has a steep, pointed prominence, very strong ridge on ala, pars descendens angled.

Bufo sp. indet.

Material. Sample HM90 T3 (5) #1713. One tibiofibula.

Rana temporaria

Material. Sample HM90 T3 (5) #1485. One left ilium. #995. One right ilium. #1021. One left ilium. #1595. One right ilium. #1402. One left ilium. #2131. One left ilium. #1169. One left ilium. #1190. One right ilium. #1366. One left ilium. #1016. One left ilium. #1187. One left ilium. #1775. One left ilium. #2069. One left ilium. #2051. One left ilium. #2015. One right ilium. #1895. One left ilium. #1627. One left ilium. HM96 #2569. One right ilium. #2579. One right ilium. #2762. One left ilium. #306. One right ilium. #206. One left ilium. #195. One right ilium. #219 (presence noted, not exhaustively studied).

Remarks. All the ilia have relatively rounded tubers, with a low vexillum. Re-examination would be worthwhile, to compare this material with other Lateglacial and Holocene fossil anuran ilia. Material from other sites appear to be morphologically distinct from most modern *R. temporaria* ilia.

LITTLE HOYLE CAVE, nr. TENBY, DYFED

This small cave (NGR SS112999) is situated 350m south of Hoyle's Mouth Cave, near Tenby. It it sometimes known as 'Longbury Bank' and is developed in a narrow ridge of Carboniferous Limestone (Campbell and Bowen, 1989). It has four entrances, three to the north and one to the south, and a central chimney connects to the surface above. The cave lies at about 20m above OD, with narrow valley floors 7m below on either side. It has a history of nineteenth century investigation, including work by Winwood, Rolleston, Laws, Boyd Dawkins and Lane Fox (General Pitt Rivers). Campbell and Bowen (1989) provided an account of the cave's excavational history. Winwood partly excavated a kitchen midden in the north chamber and most of the other work was centred on emptying the chimney of sediments. McBurney carried out more recent digging between 1958 and 1963 (McBurney, 1959), and Stephen Aldhouse-Green (National Museum of Wales) continued excavations in 1984 and 1986 (Green *et al*, 1986) and in 1990.

Green *et al* (1986) argued that the elevation of the cave (20m OD) is probably within reach of Ipswichian high sea levels, and Rolleston *et al* (1878) suggested that it may once have been entered by the sea. It is highly unlikely, however, that such a high sea level could have been attained during the Late Pleistocene (D.H. Keen, pers. comm., 1998). The sedimentary sequence is complex and varies throughout the different chambers (Campbell and Bowen, 1989). The deposits probably spanned much of the Devensian, but only a fragmentary sequence now exists (Green and Walker, 1991). The most recent work by Aldhouse-Green opened up several trenches adjacent to the chimney and on platforms at the northern and southern entrances. The stratigraphy at the northern platform (Green *et al*, 1986) was a follows:

10	Soil
9	Orange-brown clay with stones
8	Upper scree
7	Buff-grey silt
6	Stony silt
5	Pink clay
4	Middle scree
3	Orange and black clay
2	Lower scree
1	Bedrock

U-Th dating gave an age of 47,500+9,500/-8,500 years BP on a wall stalagmite (Campbell and Bowen, 1989; Green and Walker, 1991). This caps a layer of brecciated sediments beneath, containing bear and reindeer. These sediments thus appear to be Early or Middle Devensian in age and are the oldest remaining sediments in the cave (Campbell and Bowen, 1989). Most of the overlying sediments are Late Devensian thermoclastic screes, and U-Th and radiocarbon dates on

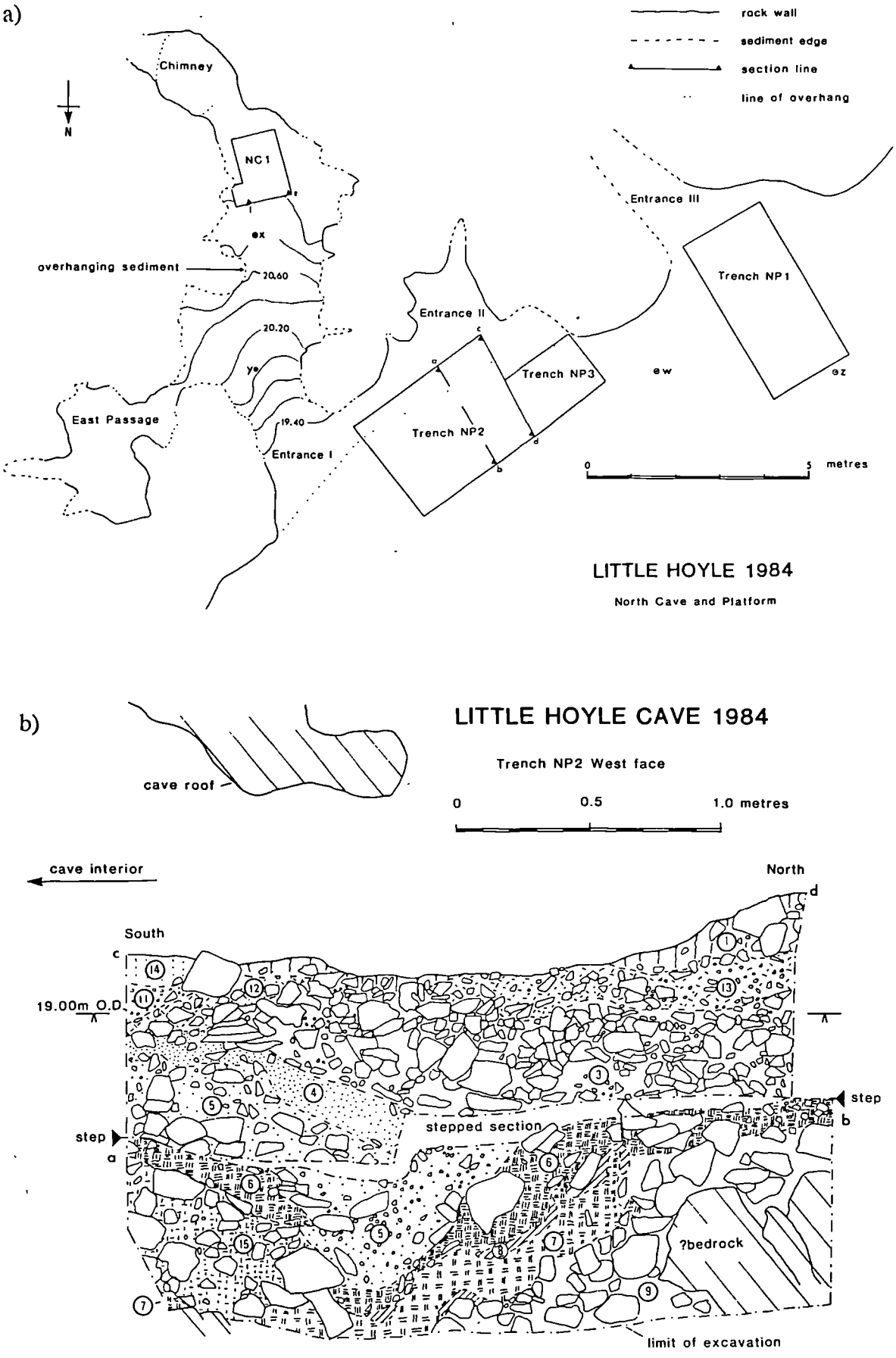


Figure 6.21: Little Hoyle Cave, Dyfed: a) Plan of cave and excavated areas; b) Lithostratigraphic section (after Green *et al*, 1986).

STRATIGRAPHY		ARCHAEOLOGY*	FAUNA	ENVIRONMENT/INTERPRETATION
Topsoil 1 14	Brown soil			
Orange clay with small stones 11 13	Orange-brown clay with mixed stones			(11) probably, (13) certainly McBurney backfill
Red Cave Earth 12 3	Upper Scree	Creswellian penknife point, large flint blade and flint chip	Dicrostonyx torquatus, Lepus cf timidus, Vulpes* sp., Ursus* sp., Rangifer tarandus*	Open treeless tundra - a harsh environment
4	Buff Grey Silt		Ursus arctos, Equus sp., Rangifer tarandus	Slight climatic amelioration but still cold and wet. Probably scrub or park tundra.
5	Stony Silt		Vulpes vulpes, Equus ferus, Microtus oeconomus	Very cold wet conditions with open grassland, possibly resembling arctic tundra
6	Pink Clay			Closed pine woodland with only limited open ground
15	Middle Scree			. Not sampled for pollen.
[illegible] 8 7	Orange Clay			Warm dry conditions, probably open grassland with considerable tracts of pine-birch-aspen' woodland
9	Lower Scree		Lepus cf timidus*	Open landscape, possibly resembling present day arctic pine-ericaceous heathlands.
Bedrock				

Table 6.10: Relationships between lithostratigraphy, archaeology and fauna at Little Hoyle Cave, Dyfed (after Green *et al*, 1986).

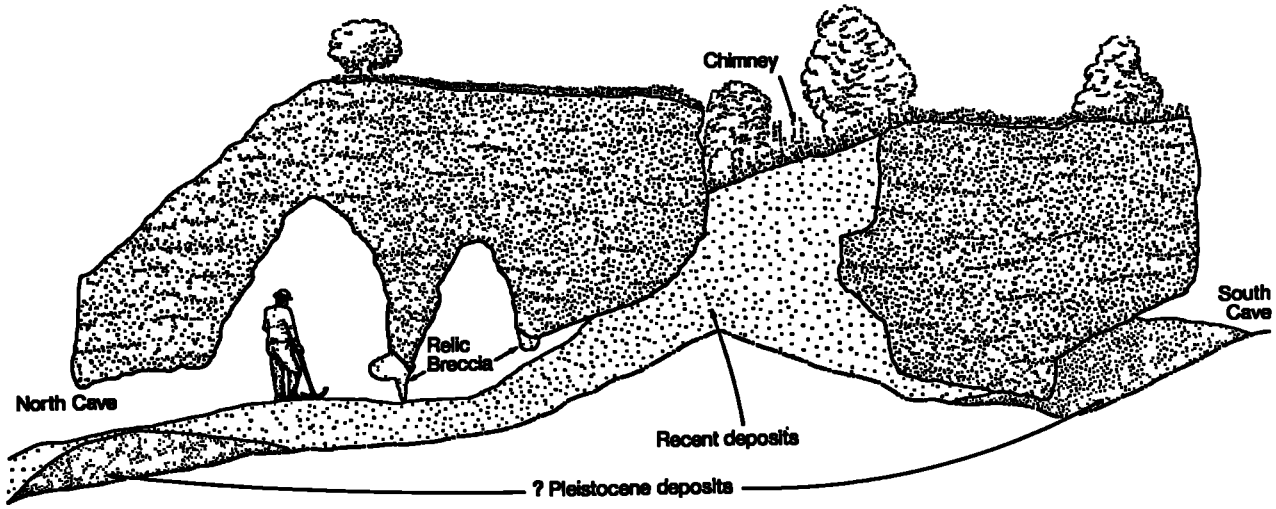


Figure 6.30: Schematic section through Little Hoyle Cave (Longbury Bank), Dyfed (after Green and Walker, 1991).

bone group closely around 18,000 BP. The associated fauna from the red sandy silt in the north chamber included brown bear, fox, reindeer, hare, arctic lemming, tundra vole and some large birds (Green *et al*, 1986). Woolly rhinoceros and mammoth were recovered by earlier workers, although they were not certainly associated with the glacial maximum fauna. Later deposits include norway lemming, northern vole and numerous barnacle goose, and probably date to the Devensian Lateglacial (Green *et al*, 1986). Pollen from the upper scree indicated a harsh tundra environment (Green and Walker, 1991). A Creswellian artefact recovered by McBurney (1959) was from Bed 8, which has been correlated palynologically to zone III (Green *et al*, 1986).

Sorted remains from the 1986 and 1990 excavations of the north chamber (Trench 5), north platform (Trench 4, Layer 3a) and south chamber (Trench 6, Layer 16) were studied at the NMW in 1996. Herpetofaunal remains were less abundant than for Hoyle's Mouth, and their age is not certain. Only anuran ilia and a few other elements were seen, belonging to *B. bufo, Bufo* sp. and *R. temporaria*. Table 6.1 shows the taxa recovered from each sample.

Table 6.11.

North Platform:		
Layer 2	#1575	*B. bufo*
(1990 excavations)	#1577	*R. temporaria*
	#1578	*R. temporaria*
	#1597	*B. bufo*
Trench 4, Layer 3a	#723	*Bufo* sp., *R. temporaria*
(1986 excavations)	#796	*R. temporaria*
	#813	*R. temporaria*
	#818	*B. bufo*
	#838	*B. bufo*
	#895	*B. bufo*
	#1000	*B. bufo*
	#1013	*R. temporaria*
North Chamber:		
Trench 5	#313	*B. bufo*
(1986 excavations)	#419	*R. temporaria*
	#420	*R. temporaria*
	#500	*R. temporaria*

South Chamber:

Trench 6, Layer 16	#94	*B. bufo*
(1986 excavations)	#121	*B. bufo*
	#131	*B. bufo*
	#263	*B. bufo, R. temporaria*
	#279	*B. bufo*
	#294	*B. bufo*
	#319	*Bufo* sp.

Systematic palaeontology

Bufo bufo

Material. Sample LH90 NP#1575. One right scapula. #1597. One right ilium. LH86 T5 NC#313. One left ilium. LH86 T4 (North)(3a) NP#723 (presence noted, not exhaustively studied). NP#895. One right ilium. NP#818. One left ilium. NP#838. One left ilium. NP#1000. One left ilium and two right scapulae. LH86 T6 (16) SC#121. One left ilium. SC#131. One left scapula. SC#94. One right ilium. SC#263. One left ilium. SC#294. One right ilium. SC#279. One right ilium.

Bufo sp. indet.

Material. Sample LH86 T16 SC#319. One left scapula.

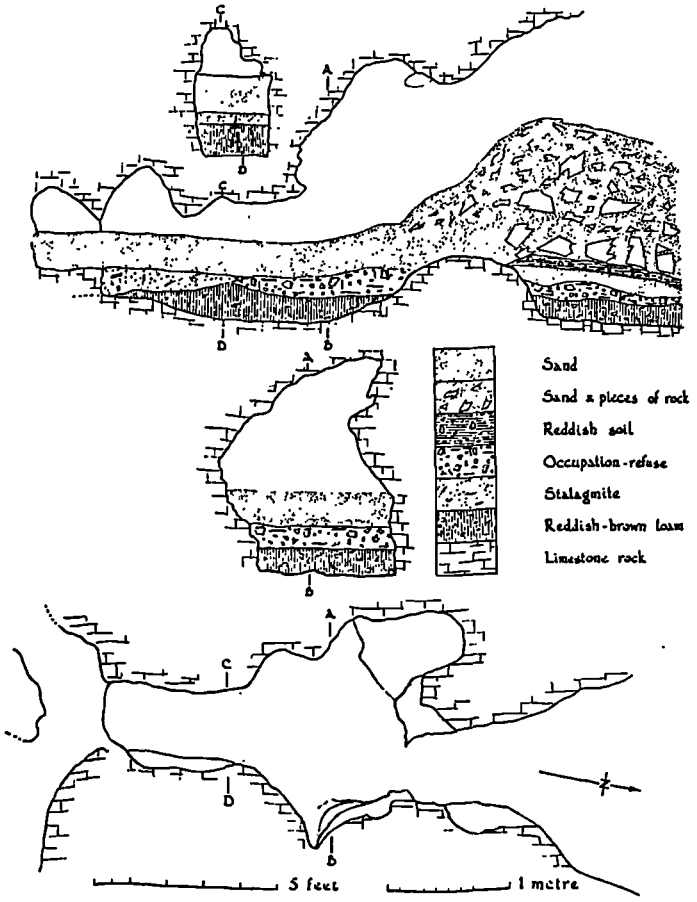
Remarks. The proximal end of this scapula exhibits unusually great thickening, including a bulbous nodule on its ventrolateral face. Its middle section is disproportionately narrow. As there appears to be pathogenic growth on this bone, the absence of a supraglenoid fossa is less safe for diagnosis, and it will be referred to *Bufo* sp.

Rana temporaria

Material. LH90 NP#1578. One right ilium. #1577. One right ilium. LH86 T5 NC#420. One right ilium. NC#419. One right ilium. NC#500. One right ilium. LH86 T4 (North)(3a) NP#723 (presence noted, not exhaustively studied). LH86 T4 NP#796. One left ilium. NP#813. One left ilium. NP#1013. One left ilium. LH86 T6 (16) SC#263. Two left ilia.

Remarks. NC#500 has an unusual fin-shaped tuber, sharpened into a point, anteriorly. There is no correspondingly high vexillum, except for a rudimentary extension to the tuber. One of the left ilia in SC#263 is only a partial specimen. All the ilia have tubers which allow their identification as *R. temporaria* with certainty.

a) POTTER'S CAVE - HIGH CLIFF - CALDEY



b)

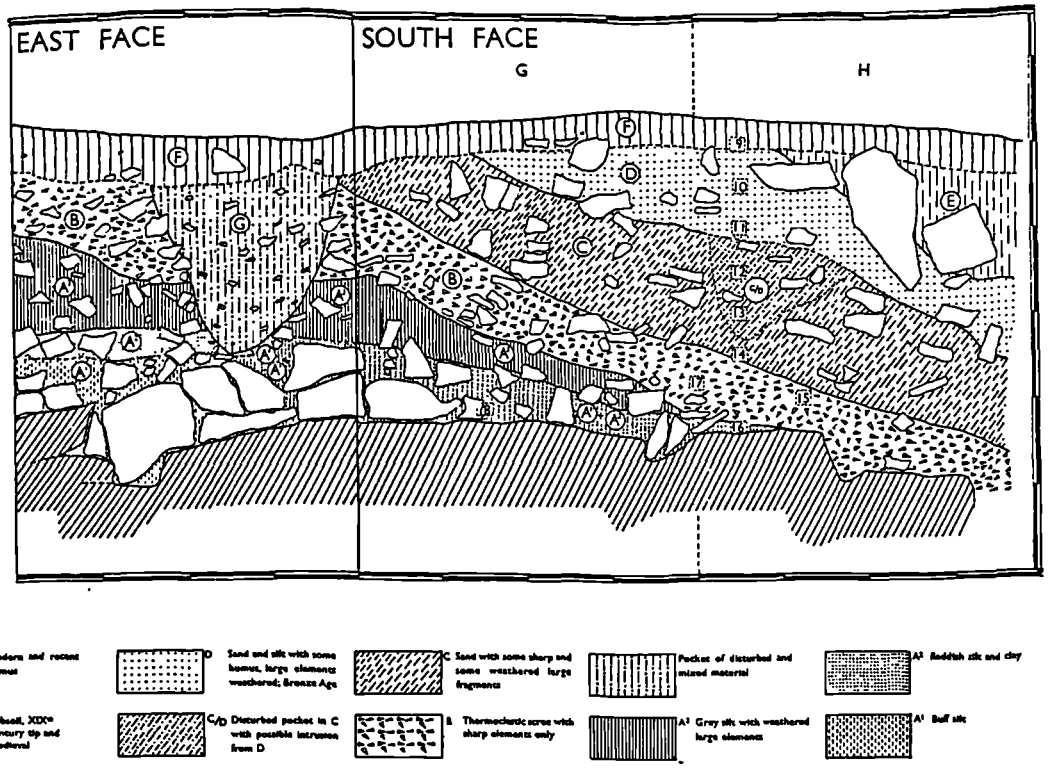


Figure 6.31 : a) Plan and sections through Late Pleistocene and Holocene deposits of Potter's Cave, Dyfed (after Lacaille and Grimes, 1955); b) Lithostratigraphic section of Lateglacial and Holocene deposits of Cathole, West Glamorgan (after McBurney, 1959).

POTTER'S CAVE, CALDEY ISLAND, DYFED

Potter's Cave (NGR SS143971), on Caldey Island in Pembrokeshire, is a small fissure with two entrances 6m apart (Davies 1989; Green and Walker, 1991). It was (re)discovered in 1950, at which time its entrances were blocked by blown sand and fallen rocks, partly caused by adjacent quarrying (Lacaille and Grimes, 1955). Excavation of the east entrance by Lacaille and Grimes over the following five years produced a mixed assortment of Neolithic, Bronze Age and Iron Age artefacts together with Holocene mammals. Beneath these deposits, a hard stalagmite layer was reached but could not be penetrated and work was abandoned. In 1973, M. Davies continued work at the cave and removed 60cm of stalagmite. He recovered hyaena teeth and what he termed 'Creswellian artefacts', viz. a backed blade and a penknife point, from a 'stony red clay' beneath the stalagmite (Davies, 1989). When excavations were moved to the west entrance and onto the sloping platform outside the cave, he recovered an array of faunal remains, including hyaena-gnawed horse bone and woolly rhinoceros within the red stony clay. Thus it appears that the deposits beneath the stalagmite were accumulating from the Middle Devensian onwards, culminating with the Late Upper Palaeolithic human presence. The stalagmite layer is therefore most likely to be of early to middle Holocene age, and probably accumulated over some time. Green and Walker (1991) suggested that the cave was not big enough for human habitation.

Small vertebrate remains from Potter's Cave were studied at the National Museum of Wales (Cardiff) in 1996. Small vertebrate remains from sample 91.10H/7 were already sorted and separated from the residue. Sample 91.7H/471 6.6.1976 was labelled 'Midden layer under Upper Stalagmite layer'. It contained a large piece of brecciated material and is thus from immediately below the stalagmite layer. The sample consisted of unsorted sieve residue and weighed c.300g. Anuran remains were not exhaustively removed from it, but the identified bones are now sub-bagged within it. Unfortunately, the newt vertebra was lost accidentally. The total herpetofaunal list is *T. vulgaris/helveticus, B. bufo, B. calamita, B.* cf. *calamita, R. temporaria, Rana* sp., Anura indet. Table 6.12 shows the taxa recovered from each of the two samples. Owing to its association with the Late Upper Palaeolithic archaeology, the age of this material is almost certainly Devensian Lateglacial (Aldhouse-Green, pers. comm., 1996). This also agrees with the inclusion of *B. calamita* in an otherwise impoverished herpetofauna.

Table 6.12.

Sample 91.7H/471 6.6.1976: "Midden layer under Upper Stalagmite layer"

T. vulgaris/helveticus, B. bufo, B. calamita, B. cf. *calamita, R. temporaria, Rana* sp., Anura indet.

Sample 91.10H/7

B. bufo, B. calamita, R. temporaria

Systematic palaeontology

Triturus vulgaris/helveticus

Material. Sample 91.7H/471 6.6.1976. One caudal vertebra (specimen lost).

Remarks. This minute specimen had relatively broad, shouldered neural and haemal spines, cf. *T. vulgaris*. However, it was partly stalagmite-encrusted, and not certainly identifiable.

Bufo bufo

Material. Sample 91.10H/7. One left ilium. Sample 91.7H/471 6.6.1976. About forty ilia, scapulae and frontoparietals, plus various other elements.

Remarks. All the ilia have been removed from sample 91.7H/471), but specimens of virtually every other skeletal element remain in the sample. Some of the ilia have relatively pointed tubers, but are still distinct from *B. calamita*. Some of the scapulae have one or two small foramina, or a slight hollow, adjacent to the glenoid cavity margin, but not as pronounced as in *B. calamita*. All are referred to *B. bufo*, and the high proportion of *B. bufo* ilia agrees with this.

Bufo calamita

Material. Sample 91.10H/7. One left and one right ilium. Sample 91.7H/471 6.6.1976. One right ilium.

Remarks. Sample 91.10H/7. Very pointed tubers. Other features not diagnostic. 91.7H/471 6.6.1976. Fairly pointed, triangular tuber. Pars descendens wide and angled, deeply undercut and with a strong spina pelvis anterior.

Bufo cf. *calamita*

Material. Sample 91.7H/471 6.6.1976. One ilium, one scapula and one sacrum.

Remarks. These elements are probably *B. calamita* also.

Rana temporaria

Material. Sample 91.10H/7. One left and one right ilium. Sample 91.7H/471 6.6.1976.

Rana sp. indet.

Material. Sample 91.7H/471 6.6.1976. Two ilia and one tibiofibula.

Remarks.The ilia are too incomplete for specific determination, but belong to *Rana.*

Indeterminate Anura

Material. Sample 91.7H/471 6.6.1976. Various elements.

CATHOLE, GOWER, WEST GLAMORGAN

Cathole Cave (NGR SS538900) is situated 2km inland from the modern coast, in the parish of Ilston on the Gower Peninsula. It was excavated during the 1860s by Wood, who recovered a large Devensian mammal fauna but kept no contextual records (Garrod, 1926; Campbell, 1977). Subsequent excavations were carried out in 1958-9 by McBurney (1959) and in 1968 by Campbell (1977). McBurney's stratigraphy is shown in Figure 6.31b. The assemblage of spotted hyaena, bear, lion, wildcat, fox, mammoth, woolly rhinoceros, horse, giant deer, red deer and reindeer is probably composite, comprising typical Middle and Late Devensian cold-climate elements. McBurney's (1959) list, with temperate elements such as roe deer, is even more mixed than Wood's (Campbell, 1977). The Palaeolithic archaeology of Cathole dates predominantly to the Lateglacial, though two tanged points may be from c.28,000 BP (Green and Walker, 1991). The mammal faunas associated with the Lateglacial occupation(s) c.12,000 BP include brown bear, arctic fox, field vole, collared lemming and wood mouse in Layer LOB, with red fox and ?reindeer in Layer MSB (Campbell, 1977; Green and Walker, 1991). The Late Upper Palaeolithic finds represent both Creswell- and Cheddar-type blades, as well as worked bone and a variety of tools. Campbell (1977) made careful biostratigraphic analyses and detailed an abrupt transition from 'Arctic-Boreal types' to 'Boreal-Temperate types' between unit USB and C, at the Lateglacial/Early Holocene boundary. Mesolithic artefacts are also known from the cave, with associated palynology indicating an early Holocene forested environment.

Small vertebrate remains from Cathole were studied during a visit to the National Museum of Wales (Cardiff) in 1996. The material studied came from the McBurney excavations of 1958. A number of bags of dirty, unwashed small bones has been partly examined for herpetofaunal remains, but not exhaustively. Bags #1-#60 from the 1958 excavation were studied, but bags #61-#202 were not examined, nor were a further #192 bags from the 1959 excavations. The bones are a creamy white colour and do not appear to be very old, but their age is uncertain.

Systematic palaeontology

Bufo bufo (Linnaeus 1758)

Material. Bag #4. One left and two right ilia. #15. One left ilium. #17. One left ilium. #94+#50. Three right ilia. Bags #55 and #60. Ilia visible, but not exhaustively studied.

Bufo sp. indet.

Material. Bag #23. Two tibiofibulae. #29. One tibiofibula.

Rana temporaria

Material. Bag #3. One right ilium. #19. One left and one right ilium. #20. One left ilium. #23. Two left and one right ilia. #15. One left ilium. #94+#50. One left ilium.

Rana sp. indet.

Material. Bag #1. One left humerus. #29. One tibiofibula.

Remarks. Both are likely to belong to *R. temporaria*, but a certain determination could not be made at the time.

PONTNEWYDD CAVE, nr. ST. ASAPH, CLWYD

Pontnewydd Cave (NGR SJ015710) is formed in the Carboniferous Limestone of the Elwy Valley in Clwyd, North Wales (Campbell and Bowen, 1989). Its elevation is c.90m OD, some 50m above the River Elwy. The cave consists of one major chamber, orientated east-west, with a southwest-facing entrance, and with several subsidiary passages. It was excavated by Boyd Dawkins and Hughes during the 1870's, who recovered fauna including a possible human tooth (now lost) and artefacts of Acheulian and Mousterian type. The cave was used as an ammunition dump during World War II, a wall was built at its entrance and inevitable disturbance of sediments occurred in the entrance area. Nevertheless, excavations by the National Museum of Wales (Cardiff), directed by Stephen Aldhouse-Green in the 1980's, uncovered a sequence of sediments spanning periods from the Late Middle Pleistocene to the present (Green *et al*, 1981). Green (1984) gave an account of the excavations, faunal and archaeological finds and stratigraphic contexts.

No complete stratigraphic sequence remains intact in the cave, but a composite section interpreted by Collcutt (1984) is shown in Figure 6.32b. The following generalised sequence was given by Green (1984):

11) Earthy Unit	(Calcareous Member)
10) Laminated Travertine	"
9) Upper Clay and Sands	"
8) Red Cave Earth	"
7) Upper Breccia	"
6) Silt	"
5) Stalagmite	"
4) Lower Breccia	"
3) Intermediate Complex	"
2) Upper Sands and Gravels	(Siliceous Member)
1) Lower Sands and Gravels	"

Uranium series dating on samples of travertine (some of them *in situ*) gave ages of c.170-180ka BP, c.125ka BP, c.90ka BP and a maximum age of 20ka BP (Green *et al*, 1981). Perhaps the most important find from Pontnewydd Cave was a single human molar which was recovered *in situ* from the 'Intermediate Complex'. A few other human remains, including two upper molars of Neanderthal affinities, were been recovered from various locations within the cave (Stringer, 1984). A number of handaxes, Levallois cores and scrapers were also recovered (Green *et al*, 1981).

The faunal remains occur in three successive lithological units and include lion, bear, a leopard-sized cat, fox, Merck's rhinoceros, horse, red deer, reindeer, beaver, pika, hare, tundra vole, lemming, northern vole and water vole (Green *et al*, 1981). This assemblage is clearly mixed. Some of the species could represent a cold climate assemblage, and the poor condition of

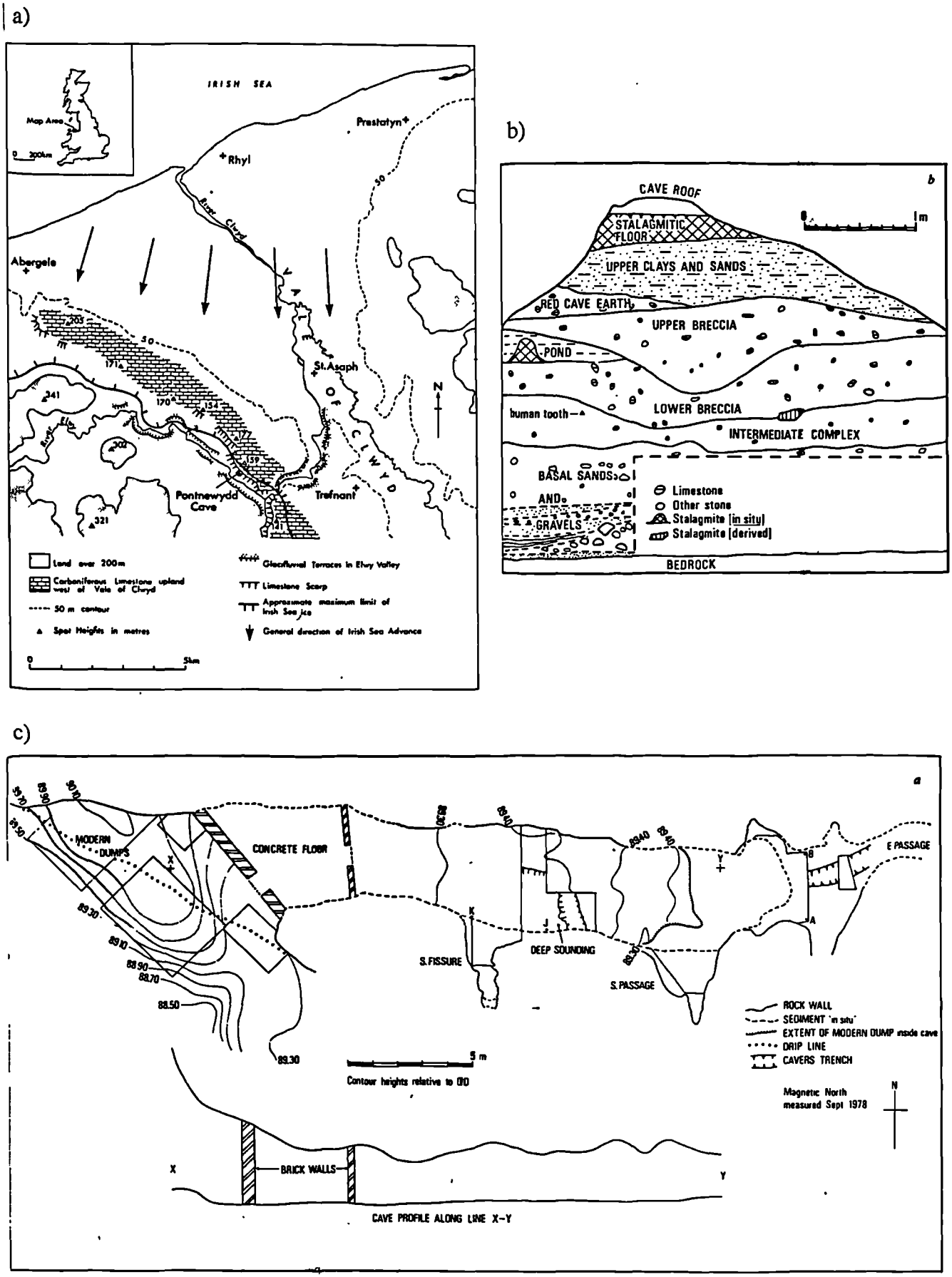


Figure 6.32: Pontnewydd Cave, Clwyd: a) Location; b) Schematic representation of lithostratigraphy; c) Survey of the cave (after Green *et al*, 1981).

the bones suggests debris-flow transport and redeposition. The records of the Ipswichian elements, hippopotamus, straight-tusked elephant, narrow-nosed rhinoceros and spotted hyaena from 19th Century excavations could not be substantiated by Green *et al*'s work and, if they are correct, they imply the presence of a localised entrance deposit not seen by Green *et al* (1981) which is now lost. Alternatively, and far more likely, the identifications might have been confused with the nearby Cefn Caves (Currant, 1984). The combination of TL and U-Th dating of human tooth and stalagmite, together with the faunal assemblage, suggests that human occupation took place some time in Stage 7 or early Stage 6 (Green *et al*, 1981).

Currant's (1984) reappraisal of the mammalian remains found that most of the material is not *in situ* and that three distinct mammal faunas could be isolated, relating to three different ages during deposition of beds in the calcareous member. The first is a 'warm' fauna in the Intermediate Complex, with bear, horse, roe deer, beaver and wood mouse, probably dating to Substage 7c (Campbell and Bowen, 1989). The second assemblage is mainly in the Lower Breccia and is dominated by bear, horse and narrow-nosed rhinoceros. It generally indicates a 'cool temperate' open steppe environment (Currant, 1984; Green, 1984), and probably dates to Substage 7b (Campbell and Bowen, 1989), during which it has been suggested that there was a short cold phase (Andrews, 1989). The third group occurs in the Pond Silt (Unit 6) and the Upper Breccia. It is a typical Arctic assemblage, including wolf, red fox, brown bear, reindeer and arctic hare. It is interpreted as the contents of a wolf den and has obvious affinities with many other faunas well -dated to the Late Devensian and Devensian Lateglacial (Currant, 1984). It seems that during the whole of Stage 6 and Substage 5e, no clastic deposition took place and the cave entrance was probably blocked (Green, 1984). No Holocene sediments or assemblages appear to have been described from Pontnewydd. Further work has been published on the earlier sequences and human remains, but this has no bearing on the age and interpretation of the herpetofauna described below.

A small sample of Red Cave Earth taken by A. Currant (Sample 'APC 1982 [D]') produced approximately 100g of sieve residue. As this unit stratigraphically overlies and post-dates the Lateglacial mammal fauna of the Upper Breccia, it can be assumed to be of Holocene age. The sample produced fairly abundant herpetofaunal remains. Not all anuran bones were removed from the sample, as no further diagnostic information could be obtained by doing so. Some further vertebrate remains from the site were also studied during a visit to the NMW in 1996. These remains were from the Upper Clays and Sands, which overlie the Red Cave Earth in Collcutt's (1984) stratigraphy, and from disturbed material associated with the WWII dump at the cave entrance (E. Walker, pers. comm., 1996). Herpetofaunal remains were found in six samples studied. Thus it appears that herpetofaunal remains can be described from two distinct Holocene units: the Red Cave Earth and the succeeding Upper Clays and Sands. No specific ages can be assigned to these units.

The total herpetofaunal list recovered from the samples seen so far is: *T. cristatus, T. vulgaris, T.* cf. *helveticus, Triturus* sp., *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura

indet., *A. fragilis, N. natrix* and *Natrix* sp. Table 6.13 shows the taxa recovered from each sample.

Table 6.13.

Upper Clays and Sands	
PN87 F1218 (surface)	*B. bufo*
PN87 F1215 (10-20cm)	*B. bufo, R. temporaria*
PN87 F1208 (20-30cm)	*R. temporaria*
Red Cave Earth	
APC 1982 [D]	*T. cristatus, T. vulgaris, T.* cf. *helveticus, Triturus* sp., *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *A. fragilis, Natrix* sp.
(poss. WWII dump, unstratified??)	
PN93 S610	*B. bufo*
PN93 S626	*R. temporaria*
PN95 A819 #2661	cf. *N. natrix*

Systematic palaeontology

Triturus cristatus

Material. APC 1982 [D]. One trunk vertebra and one left humerus.

Remarks. The anterior half of the vertebra is missing, as far as the transverse processes. Its slender shape, size, posteriorly extensive neural arch and very low neural spine identify it as *T. cristatus*. The humerus has its proximal end missing, but its distal end (and crista ventralis) is elongate, as in the *cristatus* group. It is most likely to belong, therefore, to *T. cristatus*.

Triturus vulgaris

Material. APC 1982 [D]. One trunk vertebra.

Remarks. In anterior view, its broad, shouldered posterior neural arch is indicative of *T. vulgaris*. The walls of the neural arch are spread wide and low enough to avoid any confusion with *T. helveticus*.

Triturus cf. *helveticus*

Material. APC 1982 [D]. One caudal vertebra and one cloacal vertebra.

Remarks. In anterior view, the posterior neural arch is relatively narrower and more pointed

than in *T. vulgaris*. Certain identification was not possible, however.

Triturus sp. indet.

Material. APC 1982 [D]. One anterior trunk vertebra, one middle trunk vertebra, one caudal vertebrae, one left humerus, one left femur and three ribs.

Remarks. These vertebrae belong to the *vulgaris* group, but are damaged or too small to identify. The humerus and femur have their proximal ends missing, but are small and clearly belong to the *vulgaris* group.

Bufo bufo

Material. PN93 #610. One right ilium and one left scapula. PN87 F#1218. Four left and one right ilia. PN87 F#1215. One left ilium. APC 1982 [D]. Three left and two right ilia, one left scapula, one left and two right frontoparietals, two parasphenoids, one left squamosal, five male 1st digit metacarpals, one tibiofibula, one femur and one left maxilla.

Remarks. APC 1982 [D]. The ilia have roughened and rounded tubers, clearly distinguishable as *B. bufo*. One right ilium measures 4mm, and would have belonged to a tadpole, but has a well-developed long, low, uneven tuber. The scapula is robust, with a roughened outline, and superficially similar to many *B. calamita*, but it lacks any form of depression beside the glenoid margin and is clearly *B. bufo*. The male metacarpals are large, and one displays some pathogenic growth near its proximal end. The tibiofibula is incomplete, but the nutritius foramen is not deeply excavated and the area around it is not swollen, identifying it as *B. bufo*. One left ilium from 'APC 1982 [D]' has a depression in the apex of the tuber.

Bufo sp. indet.

Material. APC 1982 [D]. One left and four right humeri, one left radioulna, one left and one right femur, one left and one right premaxilla and four distal phalanges.

Remarks. These elements probably also belong to *B. bufo*, but were not specifically identified. The left femur has a robust crest running along the proximal part of the diaphysis. The right femur is very small (3mm), and though it must have belonged to a tadpole or a metamorphosing toadlet, it has a strongly developed surface morphology. These elements belong to *Bufo*, but could not be specifically determined with certainty. Realistically, they are all probably *B. bufo*.

Rana temporaria

Material. PN87 F#1208. One right ilium. PN93 #626. One right ilium. PN87 F#1215. Two left ilia. APC 1982 [D]. Two left and one right ilia, one male right humerus.

Remarks. The ilia from the bag sample (APC 1982 [D]) have high tubers, two of them with a ribbed appearance, and two with high and continuous vexillums, deflected medially. The

humerus has strong and continuous cristata, rising in paralell, up the posterior side of the shaft.

Rana sp. indet.

Material. APC 1982 [D]. One female right humerus, one tibiofibula, one right frontoparietal, one right premaxilla, two left and three right maxillae, one sternum, one omosternum, one sacrum and one fused sacrum and trunk vertebra, four male II metacarpals and two distal phalanges. One sept-maxillary.

Remarks. The humerus lacks the diagnostic cristata of male specimens, but is of a brown frog. The frontoparietal is incomplete, preventing diagnosis. These elements probably belong to *R. temporaria* also.

Indeterminate Anura

Material. APC 1982 [D]. Various elements and fragments.

Remarks. This material was not removed from the sample, as it was not diagnostic to genus and could offer no additional information.

Anguis fragilis

Material. APC 1982 [D]. Four trunk vertebrae and four fragments of trunk vertebrae, seven caudal vertebrae, six anterior and three posterior halves of caudal vertebrae, one premaxilla, one left maxilla, one left rib and twenty-one osteoderms.

Remarks. The vertebrae are clearly distinguishable as *A. fragilis*, even as fragments. The size, shape and tooth size of the jaw elements identify them also. The rib is separable from ophidian ribs, by the less detailed morphology of the articular end.

Natrix natrix

Material. PN95 A819 #2661. One trunk vertebra.

Remarks. The trunk vertebra has a hypapophysis and neural arch characteristic of *N. natrix.*

Natrix sp. indet.

Material. APC 1982 [D]. One posterior caudal vertebra.

Remarks. This is elongate, with a fairly vaulted neural arch. The haemapophyses are broken but their bases form elongate vertical keels. The broken bases of flattened, laterally directed pleurapophyses are visible. The neural spine is long and of medium height.

6.4 Fens and East Anglia

FENLAND MANAGEMENT PROJECT SITES

During 1996 and 1997, as part of its 'Pool Frog (*Rana lessonae*) Species Recovery Programme', English Nature commissioned herpetofaunal analyses of small vertebrate remains from a number of Fenland sites, in the hope of finding subfossil remains of *R. lessonae*. The sites had been excavated archaeologically as part of the Fenland Management Project (FMP) coordinated by English Heritage. The FMP has been in operation since the 1980's and involves county archaeological units from Norfolk, Lincolnshire and Cambridgeshire, as well as various specialists. Around forty archaeological sites in the three counties were surveyed and excavated. The work was coordinated by P. Murphy (University of East Anglia) and involved multidisciplinary teams. The ages of the sites are known from their archaeological contexts, ranging from Middle Holocene (Late Neolithic and Bronze Age) to Late Holocene (Iron Age, Roman and Saxon) in age. Most of the sites are as yet unpublished, but interim reports have been written for some sites. Final reports on the archaeological, faunal and floral work for individual sites are in preparation by the relevant County Councils' archaeological units. T. Lane (Heritage Lincolnshire) is currently compiling a volume on the FMP as a whole. P. Murphy very kindly permitted study of the herpetofaunal material. T. Lane, D. Trimble (Heritage Lincolnshire), D. Gurney (Norfolk Landscape Archaeology) and U. Albarella (University of Birmingham) very kindly provided information on the sites studied.

Material from eleven of the forty or so FMP sites has been studied. Figure 1 shows the site locations. Ten of the sites, in Norfolk, Lincolnshire and Cambridgeshire, have produced herpetofaunal remains. Only Thurlby, a Roman site in Lincolnshire, did not yield any herpetofaunal remains. Material from Holme Fen and Parsons Drove in Cambridgeshire, which was studied by Irving (1995), has not been seen. All herpetofaunal remains have been removed and identified from the samples studied, except where specified (i.e. one Deeping Fen sample). Many of the sorted samples contain small mammal, bird and fish bones which have not yet been identified. Preservation of the amphibian and reptile bone is variable between sites, but is generally good though with typical patterns of breakage. The bones from Deeping Fen are particularly fragmented and coated in ironstained dust. Though fragmentation is commonplace in most of the material, the preservation of fine features suggests that little post-mortem transport has taken place. The assemblages are likely to have accumulated from animals living and dying locally. Several bones of *R. temporaria* and *B. bufo* were submitted for microsatellite DNA analysis by T. Beebee (University of Sussex), with the aim of ascertaining whether individual species can be recognised by their DNA 'signature'. The analyses were unable to isolate recognisable DNA from the bones (Beebee, 1997b).

The assemblages are detailed in full below with a site account for each locatility. Sample numbers are those used in the FMP excavations. For the Norfolk sites, the first five numbers are

sites codes allocated by Norfolk Archaeological Unit. All sites have a three-letter abbreviated name (e.g. DEN for Deeping Fen Barrow). These are followed, respectively, by the date of the excavation (e.g. 91 for 1991), the sample number ('#' with 1, 2 or 4 digits) and the context sampled (3 digits). Some samples do not have a context number and were presumably bulk samples of several contexts or a whole feature. The material is currently in the author's possession but will be returned for curation at the respective County Museums.

WARDEY HILL, COVENEY, CAMBRIDGESHIRE

This site is a Iron Age (c.2,500-2,000 BP) ringwork hillfort, on the South Bedford Level, near the village of Coveney, 7km west-northwest of Ely in Cambridgeshire (NGR TL 47808210). It has large defences with internal circular structures (T. Lane, pers. comm., 1997). It was excavated by Cambridgeshire County Council Archaeology Unit in 1991. No other site details or contextual information is known at present.

Ninety-three bags of small vertebrate remains have been examined, of which forty-one have produced herpetofaunal remains. Several of the bags duplicate the same sample numbers. The following herpetofaunal taxa were recovered: *T. cristatus, Triturus* sp., *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *A. fragilis, N. natrix,* Ophidia indet. The species recovered from each sample are listed in Table 6.14.

Table 6.14.

COY 91 #1 063	*B. bufo, Bufo* sp., *R. temporaria,* Anura indet.
COY 91 #1 245	*Triturus* sp., Anura indet.
COY 91 #1 246	*Rana* sp., Anura indet.
COY 91 #1 249	*Rana* sp.
COY 91 #2 020	*B. bufo, Bufo* sp., Anura indet., *N.* cf. *natrix*, Ophidia indet.
COY 91 #2 021	*B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet, *N. natrix*
COY 91 #2 024B	*Bufo* sp., Anura indet.
COY 91 #2 035	*T. cristatus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., Ophidia indet.
COY 91 #2 083	*B. bufo, Bufo* sp., *R.* cf. *temporaria,* Anura indet.
COY 91 #2 ?227 (sic)	*T. cristatus, B. bufo, Bufo* sp., *Rana* sp., Anura indet., *N. natrix*
COY 91 #6 206	*Bufo* sp., *Rana* sp., Anura indet.
COY 91 #36 221	*Bufo* sp., Anura indet.
COY 91 #6 225	*T. cristatus,* Anura indet.
COY 91 #6 236	*Rana* sp.
COY 91 #12 146	*Bufo* sp., *Rana* sp., Anura indet.
COY 91 #20 436	*Triturus* sp.

COY 91 #20 444	Anura indet.
COY 91 #25 315	Anura indet.
COY 91 #25 332	*Rana* sp., Anura indet.
COY 91 #25 336	*Rana* sp., Anura indet.
COY 91 #25 306	*T. cristatus, Bufo* sp., *Rana* sp., Anura indet.
COY 91 #26 359	*Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *N. natrix*
COY 91 #25/26 329	*B. bufo, Bufo* sp., *Rana* sp., Anura indet., *N.* cf. *natrix*
COY 91 #33 100	*Triturus* sp., *B. bufo, Rana* sp., Anura indet.
COY 91 #37 320	*B. bufo,* Anura indet.
COY 91 #37 328	*Bufo* sp., *Rana* sp.
COY 91 #37 630	*Rana* sp., Anura indet., *A. fragilis*
COY 91 #65 304	Anura indet.
COY 91 #80 414	*B. bufo, Bufo* sp., Anura indet., *N. natrix*
COY 91 #81 458	*Rana* sp.
COY 91 #102 508	*Bufo* sp., Anura indet.
COY 91 #102 512-514	Anura indet.
COY 91 #107 550	*Bufo* sp., Anura indet.

Systematic palaeontology

Triturus cristatus

Material. COY 91 #2 035. One sub-adult trunk vertebra. #2 ?227 (sic). One anterior trunk vertebra. #6 225. One juvenile trunk vertebra. #25 306. One immature trunk vertebra.

Remarks. #2 ?227. The anterior trunk vertebra is conspicuously large, measuring 4.0mm in length (see Figure 6.34a). It must have belonged to an animal between 160-170mm in total length. This is an exceptional size, only attained by females (Arnold and Burton, 1978).

Triturus cf. *cristatus*

Material. COY 91 #6 225. One metapodial.

Remarks. This is clearly from a large newt, and almost certainly belongs to *T. cristatus* (rather than *T. marmoratus*). It is flattened distally, with a distinct furrowed muscle scar on its ventral surface. The proximal articulation is indented ventrally, connected with the ventral fossa.

Triturus sp. indet.

Material. COY 91 #33 100. One partial left femur. #20 436. One femur. #1 245. One partial juvenile femur.

Remarks. COY 91 #33 100. Only the proximal half is intact, but it is identical in size and form to recent *T. vulgaris* group femora. Nevertheless, it could also belong to a juvenile *T.*

cristatus. #20 436. The femur is c.5mm in length.

Bufo bufo

Material. COY 91 #37 320. One sacrum. #2 83. One right ilium. #2 021. One left ilium. #2 035. One left ilium. #2 ?227. One left ilium (juvenile). #37 238. One right scapula. #2/26 329. One left ilium (juvenile). #1 063. On left ilium. #80 414. One partial left frontoparietal, one partial left squamosal and one partial right squamosal. #2 020. One left scapula.

Remarks. COY 91 #2 83. The ilium has a very prominent, shouldered tuber (see Figure 6.34b). This is fairly distinctive, and comparable to *B. bufo* from Deeping Fen. #2 021. The ilium has a low tuber and an unusually thin ala base. #2 035. The ilium has a fairly triangular tuber, but it is laterally protrusive and irregular. Its ala is missing. #2 ?227. The juvenile ilium has an elongate, but well-developed tuber. #25/26 329. Typically large tuber, as characteristic of juvenile *B. bufo*. #1 063. This ilium has a very elongate, relatively low tuber, with several indentations. The angle between ala and pars ascendens is very obtuse, and there is a strong ventrolateral crista on the ala, but this clearly belongs to *B. bufo*. #80 414. The frontoparietal has an unusual (perhaps pathogenic) growth over the dorsal sulcus.

Bufo sp. indet.

Material. COY 91 #26 359. One tibiofibula. #25/9 329. One right humeral fragment. #6 206. One tibiofibula and one left humerus. #2 83. One femoral fragment. #2 021. One partial right squamosal, two tibiofibulae, one partial tibiofibula, two juvenile tibiofibulae, one partial tibiale, one partial fibulare, one partial femur, one radioulna fragment, one partial juvenile right ilium and one ilial ala fragment. #2 035. One radioulna. #2 ?227. One juvenile tibiofibula fragment. #25 306. One partial left angulosplenial. #37 320. One left angulosplenial. #12 146. One partial left humerus and one partial coracoid. #6 221. One tibiofibula fragment. #25/26 329. One left humerus. #107 550. One tibiofibula fragment (juvenile). #2 024B. One partial fibulare (juvenile). #102 508. One partial left humerus, one partial femur and one partial ilial ala. #33 100. One right scapula. #1 063. One right humerus and one ilial ala fragment. #80 414. One juvenile femur and one juvenile tibiofibula. #2 020. One juvenile femur, one juvenile right humerus and one left ilial ala. #2 035. One partial juvenile/larval tibiofibula.

Remarks. COY 91 #26 359. The tibiofibula has a deep groove extending from the foramen nutritius, as in *B. calamita*, but as this is a juvenile, specific determination is not possible. #2 ?227. The fragmentary tibiofibula is minute, and probably belonged to a metamorphosing toadlet of less than 20mm total length. #2 035. This is probably from a pre-metamorphosed larva.

Rana temporaria

Material. COY 91 #26 359. One ilial ala fragment and one left frontoparietal. #2 021. One left ilium. #2 035. One partial right ilium. #33 100. One ilial ala fragment. #1 063. One left ilium

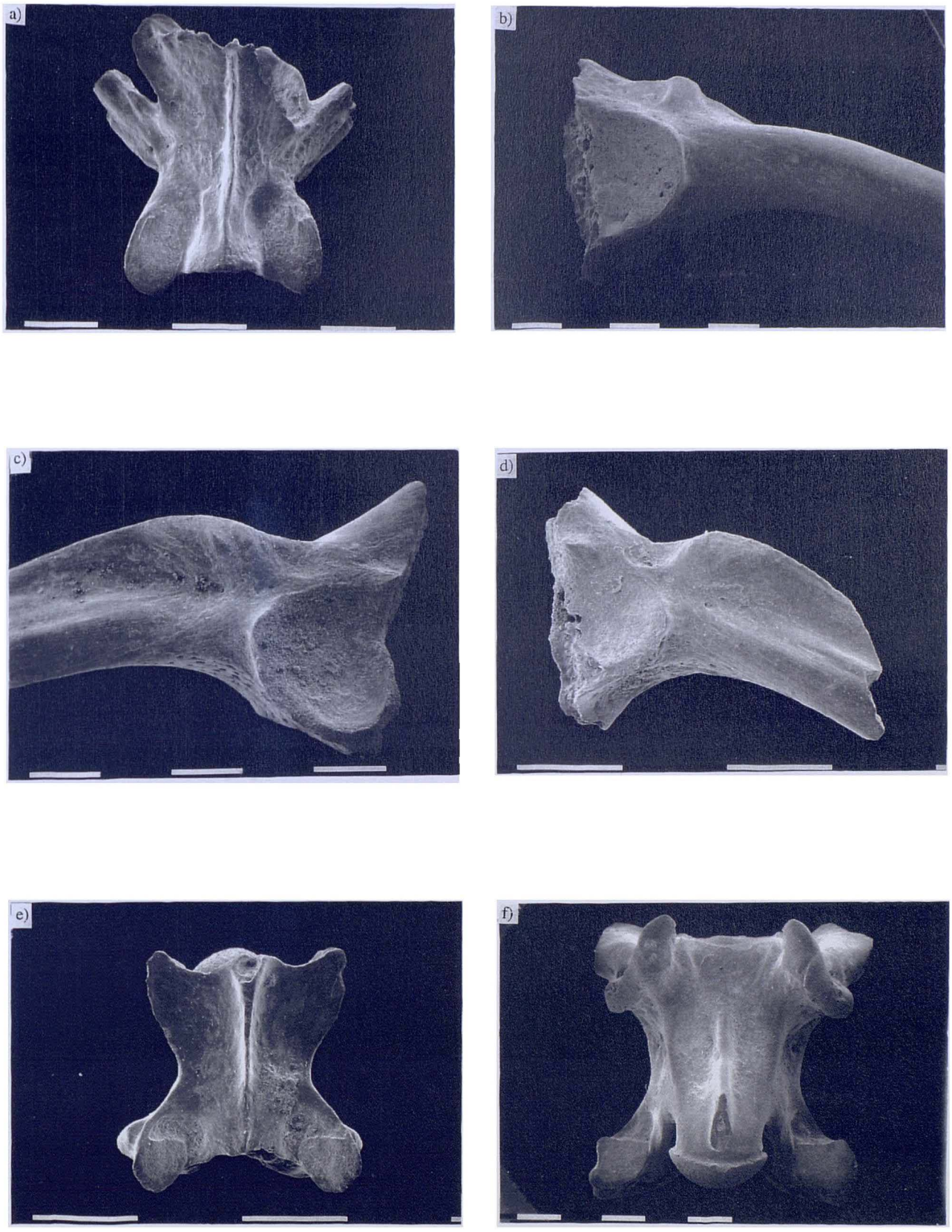


Figure 6.34: Herpetofaunal remains from Coveney: a) trunk vertebra (dorsal view) of *T. cristatus* (sample COY91 2 227); b) right ilium (lateral view) of *B. bufo* (sample COY91 2 83); c) left ilium (lateral view) of *Rana* cf. *temporaria* (sample COY91 F2 035); d) right ilium (lateral view) of juvenile *Rana* cf. *temporaria* (sample COY91 2 83); e) trunk vertebra (dorsal view) of *A. fragilis* (sample COY91 37 630); f) trunk vertebra (ventral view) of *N. natrix* (sample COY91 2 227).

(juvenile).

Remarks. COY 91 #26 359. The partial ilium is distinct as it has a thick, low, medially recurved vexillum. #2 021. The ilium has a fairly continuous vexillum, but has a high, steep and strongly ribbed tuber. The pars ascendens is missing. #2 035. The partial ilium has a thick tuber, with a protrusive, bulbous rib. The vexillum is thick and indented basally. #1 063. This case is unusual for a *R. temporaria* juveniles, and rare to find in fossil or recent form (cf. Deeping Fen sample DEN 28/91 #14 657). The tuber is fairly triangular, smooth and prominent. There is no vexillum as such, and the anterior side of the tuber slopes almost as steeply as the posterior side. There is a pre-acetabular fossa in this specimen. The only recent *R. temporaria* juveniles which have been examined (CGO 2/29 and 2/30) have high, thin vexilla. These may be a distinct form and it cannot be ruled out that other more typical *R. temporaria* normally have triangular tubers in juvenile stages.

Rana cf. *temporaria*

Material. COY 91 #2 83. One juvenile right ilium. #2 035. One left ilium.

Remarks. COY 91 #2 83. The ilium has a continuously high vexillum, with an unusually widely flared tuber. It is somewhat similar to a green frog, but the vexillum ought to be higher. It is not laterally bulbous and the junctura is thin, but this is a juvenile specimen (see Figure 6.34d). The posterior edge of the tuber is steep and its dorsal corner is quite angular. #2 035. The left ilium has a shallow-sloping, ribbed tuber and a thin vexillum (see Figure 6.34c).

Rana sp. indet. (brown frog)

Material. COY 91 #2 035. One juvenile right ilium. #26 359. One partial left ilium, one left and one right ilium. #25/26 329. One partial right ilium (juvenile).

Remarks. COY 91 #2 035. The tuber of the juvenile ilium is broken, but its vexillum is other wise intact.. The vexillum is fairly low and thin, and the junctura is very slender. These ilia also have fairly deep supra-acetabular fossae, and a small pre-acetabular fossa. #25 359. The ilia are not distinct enough to allow confident separation from *R. arvalis*. The left ilium is probably *R. temporaria* but has a broken vexillum. The right ilium has a three-ridged tuber, and may be *R. temporaria*, but its junctura is very thin. #25/26 329. This right ilium has most of its vexillum missing, but the tuber appears to be 'folded' medially, and there is a deep pre-acetabular fossa.

Rana sp. indet.

Material. COY 91 #1 246. One tibiofibula, one metacarpal and one fragmentary right maxilla. #1 249. Two femora and one tibiofibula. #26 359. One right ilium, two tbiofibulae fragments, two right scapulae and several small long bone fragments. #6 206. Two femora, one tibiofibula, one tibiofibula fragment and one right humerus. #2 021. One partial tibiofibula, one tibiofibula fragment, one partial femur, one right ilial ala fragment. #2 035. One ilial ala fragment,

one distal pesal phalanx, one femoral fragmet and one tibiofibula fragment. #81 458. One tibiofibula. #2 ?227. Two maxillary fragments, one juvenile sacrum, one partial tibiofibula, one juvenile femur and one femoral fragment. #37 238. One tibiofibula fragment, one femoral fragment and one metacarpal. #1 246. One left angulosplenial. #1 249. One partial left and one partial right angulosplenial. #12 146. One left scapula and two tibiofibula fragments. #6 236. One distal phalanx. #25 332. One left and one right scapula, and one trunk vertebra. #37 630. One partial tibiofibula. #25 336. One partial tibiofibula. #25 306. One partial tibiofibula. #25/6 329. One partial left angulosplenial. #25 332. One partial tibiofibula. #37 630. One femur.

Remarks. COY 91 #25/6 329. The ilium has a damaged tuber and vexillum, preventing identification. #2 021. The partial tibiofibula is apparently curved, as in the green frogs, but this is not certainly diagnostic. The ilial fragment has a vexillum which might not belong to *R. temporaria.*

Indeterminate Anura

Material. COY 91 #1 246. One urostyle. #37 320. Two phalanges and one humeral shaft. #20 444. One sphenethmoid and one juvenile trunk vertebra. #25/6 329. One partial right angulosplenial, one tibiofibula fragment and one partial sacrum. #6 206. One humerus. #2 83. One tibiofubula fragment. #2 021. One humeral fragment, one humeral shaft, one tibiofibula and two vertebral fragments. #2 035. One humeral shaft fragment, one right humerus, one juvenile right humerus, one humeral fragment and one juvenile radioulna. #65 304. Three phalanges. #2 ?227. One radioulna. #6 225. One humeral shaft fragment and one indeterminate limb bone. #12 146. One left humerus (juvenile), one humeral shaft and one phalanx. #6 221. One urostyle (juvenile) and one phalanx. #25/26 329. One phalanx and one partial phalanx. #25 332. One radioulna, two partial radioulnae, one urostyle, one coracoid fragment and two vertebral fragments. #107 550. One tibiofibula fragment (juvenile). #2 024B. One radioulna. #102 508. One indeterminate bone (phalanx?). #102 512-514. One radioulna (juvenile). #33 100. One metapodial (juvenile), one urostyle, one phalanx, one precoracoid and one partial pterygoid. #37 630. One partial metapodial or phalanx. #1 063. One vertebral fragment and one urostyle. #25 336. One partial male humerus (juvenile). #25 315. One radioulna. #25 306. One vertebral fragment. #2 020. One partial larval humerus. #25/6 329. One partial juvenile urostyle. #1 245. One partial urostyle. #25 332. One partial left humerus. #37 630. One left exoccipital.

Remarks. COY 91 #2 020. The humerus has its proximal end missing, but by the size of the distal portion (2mm), this must belong to a pre-metamorphosis larva.

Anguis fragilis

Material. COY 91 #37 630. One trunk vertebra.

Remarks. This is from a sub-adult specimen and is shown in Figure 6.34e.

Natrix natrix

Material. COY 91 #26 359. One trunk vertebra. #2 ?227. One trunk vertebra. #80 414. Two trunk vertebrae.

Remarks. COY 91 #26 359. The vertebra is not particularly vaulted, but its hypapophysis is of typical *N. natrix* form. Thus, it is probably a posterior trunk vertebra. #2 ?227. The trunk vertebra measures 6.4mm in length and must have come from an individual of at least 960mm in total length. It is shown in Figure 6.34f.

Natrix cf. *natrix*

Material. COY 91 #2 020. One trunk vertebra. #25/6 329. One rib. #2 021. Two trunk and one caudal vertebra.

Remarks. COY 91 #2 020. The zygosphene is very robust and noticeably domed. The parapophyseal processes are short, rounded, somewhat flattened and strongly anteriorly directed. The posterior neural arch is very rounded, perhaps suggesting a position in the anterior part of the trunk. #2 021. These vertebrae are badly damaged. The hypapophyses of the trunk vertebrae are incomplete, but they have highly vaulted posterior neural arches. The caudal vertebra has short haemapophyses, and a high neural arch.

Indeterminate Ophidia

Material. COY 91 #2 020. One juvenile vertebra. #2 035. One partial rib.

Remarks. COY 91 #2 020. The hypapophysis is broken. The neural arch is relatively low, but is not distinct enough to distinguish between *Vipera* and *Natrix*. #2 035. The rib has a pathological swelling around its proximal end which prevents further diagnosis.

LITTLE DUKE FARM, DEEPING ST. NICHOLAS, LINCOLNSHIRE

This site is on permanent pasture adjacent to Little Duke Farm on Deeping Fen (part of the North Bedford Level), in the parish of Deeping St. Nicholas, 9km south-southwest of Spalding in Lincolnshire (NGR TF 17411316). It is a Bronze Age multi-phase barrow (c.4,000-2,500 BP), built on a gravel promontary of the lower Welland Valley/fen-edge interface (French, 1994). It was excavated by Heritage Lincolnshire in 1991, under the direction of C. French, and a detailed report on the excavations and preliminary results was given by French (1994). Its site code is 28, i.e. the twenty-eighth site recognised in the parish, during the English Heritage Fenland Survey in 1986.

The site consists of a complex system of Bronze Age ring ditches, pits, graves, post-holes and other features, infilled with soil and organic remains (see Figure 6.33). Underlying these phases of activity, there is evidence of Neolithic occupation and clearance (French, 1994). Three human skeletons were found, as well as poorly preserved remains of horse, cattle, sheep/goat, pig, cat, red deer and field vole (Luff in French, 1994). Sieved samples of soil from beneath the barrow produced most of the small vertebrate bones which were identified as field vole, water vole, shrew and frog/toad. As construction of the barrow began during the early Bronze Age, the age of the faunal remains from the soil beneath is likely to be Late Neolithic, i.e >4,000 BP (D. Trimble, pers. comm., 1997). Context 657, probably material disturbed by small-scale 19th Century gravel excavation was also reported to contain a large number of frog/toad bones (French, 1994). Radiocarbon ages show that the first inhumation and associated features were dug during the very Early Bronze Age, between 3,980-3,725 BP. The mound was abandoned and 'engulfed in peat' during the Late Bronze Age between 3,210-2,950 BP. During the Neolithic, the site would have been the last (at least seasonally dry) promontary at the edge of the developing marine/freshwater fen succession (French, 1994).

Thirteen bags of small vertebrate remains have been examined in the current study, but only four have produced herpetofaunal remains. The following herpetofaunal assemblage was recovered: *T.* cf. *cristatus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *N. natrix*. Sample DEN 28/91 #14 657 consists of c.300g of sorted fragmentary bone material. This sample is the infill from the 19th Century pit, Feature #639. The abundant anuran material is very fragmentary, ironstained and apparently contemporary with (Bronze Age) or earlier than (Late Neolithic) the barrow activity. Sample DEN 28/91 #25 050 is soil fill from a female grave (Bronze Age), Feature #46. The other samples are soil from beneath the barrow and are thus probably Late Neolithic (Trimble, pers. comm., 1997). The species obtained from each sample are listed in Table 6.15.

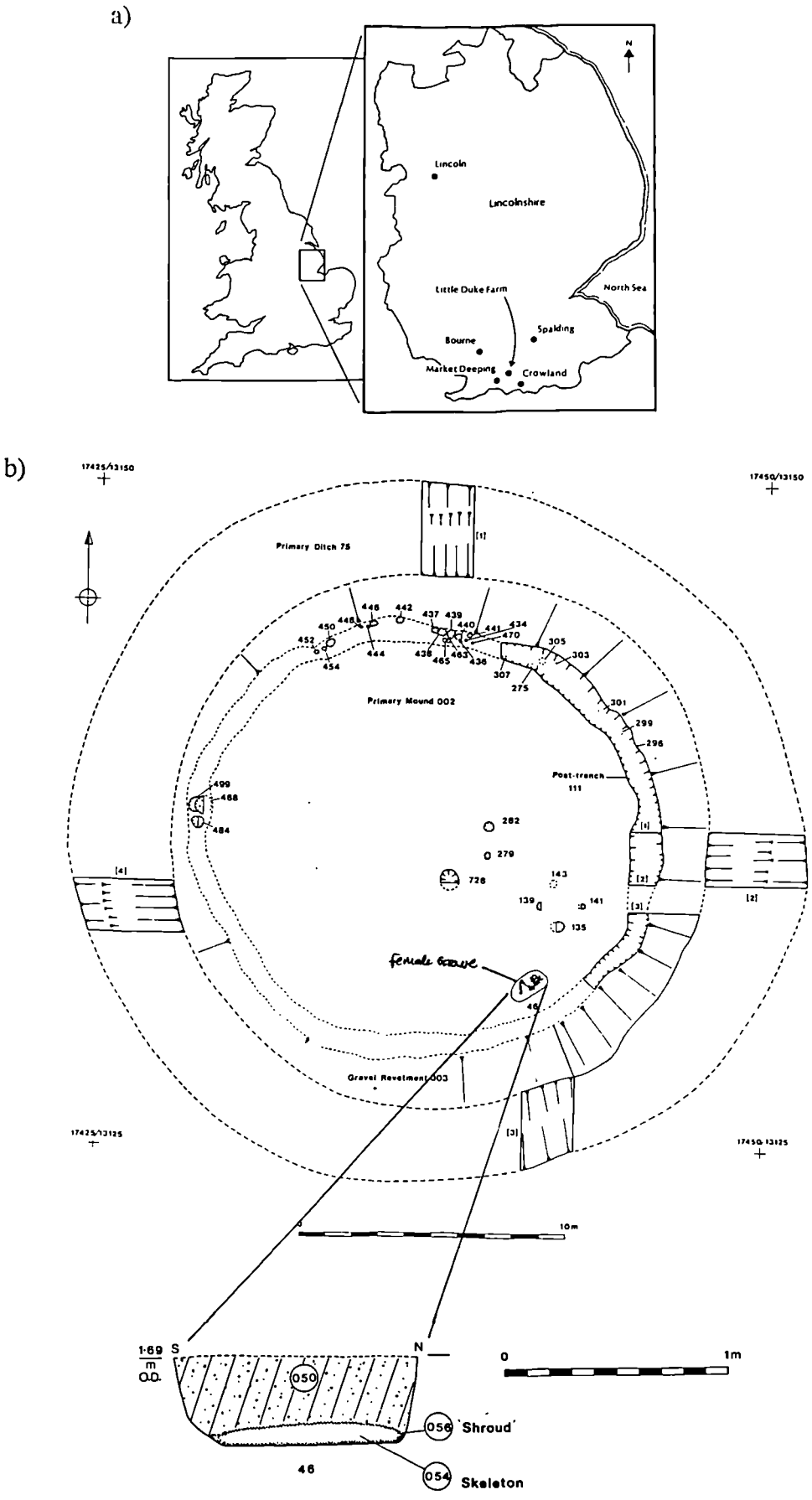


Figure 6.33: Deeping St. Nicholas, Lincolnshire: a) Location; b) Bronze Age Barrow, with (enlarged) female grave (after French, 1994).

Table 6.15.

(Bronze Age - disturbed fill from 19th Century gravel pit, Feature #639)	
DEN 28/91 #14 657	*T.* cf. *cristatus, B. bufo, Bufo* sp., *R. temnporaria, Rana* sp., Anura indet.
(Bronze Age - Soil fill from female grave, Feature #46)	
DEN 28/91 #25 050	Anura indet.
(Late Neolithic? - Soil beneath Bronze Age barrow)	
DEN 28/91	*B. bufo*
DEN 28/91 #33 087	*Bufo* sp., cf. *N. natrix*

Systematic palaeontology

Triturus cf. *cristatus*

Material. DEN 28/91 #14 657. One left pterygoid.

Remarks. From its size (4.0mm), this is clearly not from a *vulgaris* group species, and belonged to an animal of c.140mm in total length. It is very different in shape from *S. salamandra*, which has a much wider posteromedial process. *T. marmoratus* has its ventral cristata produced ventrolaterally into a thin lamina. Its posteromedial process is also narrower and produced. The fossil specimen has better developed ventral cristata than the recent *T. cristatus* seen, but is otherwise indistinguishable from this species. It probably came from a mature female specimen.

Bufo bufo

Material. DEN 28/91 #14 657. Twenty-nine left and twenty right ilia, one left and four right scapulae, one sacrum and one atlas vertebra. DEN 28/91. One left ilium (submitted for DNA analysis).

Remarks. These bones are all in poor condition, with varying amounts of breakage. They are ironstained with a reddish brown colour. The tuber shapes are unusual: generally elongate, with a rounded profile, but with a narrow, horizontally constricted lateral protuberance bordered by depressions on the anterolateral and posterolateral sides. One or two are almost identical to the 'unusual form' described by Holman (1989), from West Runton, Norfolk. One has a very narrow, dorsally protrusive tuber, though with a shouldered apex (see Figure 6.35b). Another has a very rounded profile, but an almost concave lateral side. It is still distinguishable from *B. calamita*, by

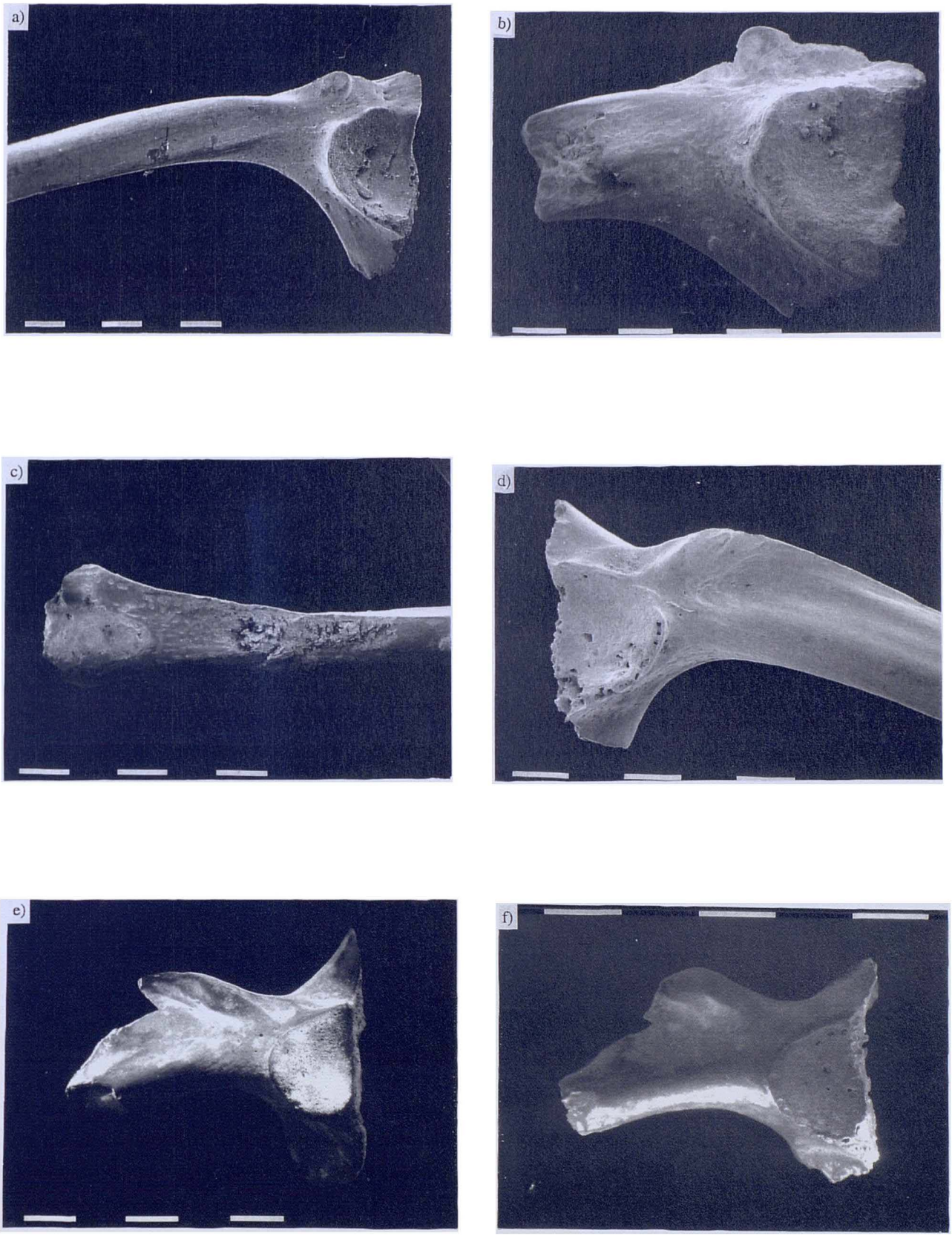


Figure 6.35: a) Left ilium (lateral view) of *B. bufo* from Whitemoor Channel (NCM 143.949 WC96-98; i.e. the '*B. calamita*' of Holman and Stuart, 1991); b) left ilium (lateral view) of *B. bufo* from Deeping St. Nicholas (sample DEN 28/91); c) right humerus (posterior view) of male *Rana* cf. *temporaria* from Gosberton Mornington House (sample GOS93 36 142); d) right ilium (lateral view) of *Rana* sp. (brown frog) from Gosberton Mornington House (sample GOS93 9 021); e) left ilium (lateral view) of *Rana arvalis/dalmatina* from Gosberton Chopdike Drove (sample GOS92 65 596); f) left ilium (lateral view) of *Rana* cf. *arvalis* from Terrington St. Clement (sample 22275 TSC 3 22).

the large area covered by the base of the tuber. The atlas is large, very robust and somewhat laterally compressed. Several of these elements are from large adults.

Bufo sp. indet.

Material. DEN 28/91 #33 087. Two femora and one partial left ilium. DEN 28/91 #14 657. Fifteen partial tibiofibulae, one tibiofibula, one six male left and one male right humerus, one female left and one female right humerus, seven left and nine right humeri, one juvenile humeral shaft, one radioulna, two trunk vertebrae, two partial right ilia, two ilial fragments, six ilial ala fragments, one right premaxilla, one partial squamosal, one femur, two femoral fragments, one right scapula and one scapula fragment. A large number of partial *Bufo* humeri and numerous other recogniseable fragments have not been removed from the sample residues.

Rana temporaria

Material. DEN 28/91 #14 657. One left and two right ilia, one juvenile left ilium and a tibiofibula.

Remarks. Right ilium has a ribbed tuber and an icomplete, but depressed vexillum. Left ilium (juvenile) has a smooth, almost triangular tuber, with no real vexillum. This is an unusual form in *R. temporaria* (cf. also Coveney: COY 91 #1 063). All other species have a higher, thinner and more continuous vexillum than *R. temporaria*, which normally has at least some form of low vexillum.

Rana cf. *temporaria*

Material. DEN 28/91 #14 657. One right ilium (submitted for DNA analysis).

Remarks. This ilium has a ribbed tuber and is apparently *R. temporaria*. However, as the vexillum is broken, identification is not certain.

Rana sp. indet.

Material. DEN 28/91 #14 657. One male right humerus.

Indeterminate Anura

Material. DEN 28/91 #25 050. One radioulna fragment. DEN 28/91 #14 657. Four humeral fragments, two distal right humeral fragments, one partial ilium, three ilial fragments, one ilial ala fragment, five vertebral fragments, four phalanges, two radioulnae, one radioulna fragment, one tibiofibula fragment and one fibulare.

cf. *Natrix natrix*

Material. DEN 28/91 #33 087. One incomplete left rib.

Remarks. The distal part is missing, but the articular end is almost complete. It is easily

distinguished from *A. fragilis*, has a different articular shape to *V. berus*, and lacks the anterior bulb on the ventral part of the articular end in *C. austriaca.* It is not identical to recent *N. natrix* with which it has been compared, but this may be due to intracolumnar variation. The dorsal process of the articular end is slightly anteriorly directed.

LEAVES LAKE DROVE, PINCHBECK, LINCOLNSHIRE

This is an Early to Middle Saxon settlement (c.1,600-1,200 BP), close to Leaves Lake Drove (i.e. a cart track) near the village of Pinchbeck, 3km north of Spalding in Lincolnshire (NGR TF 19212510). The site was excavated by Heritage Lincolnshire in 1994, under the direction of T. Lane. It is characterised by infilled ditches and pits, and a feature interpreted as a contemporary pond (T. Lane, pers. comm.). No further contextual information is known at present.

Sixteen bags of small vertebrate remains have been examined, of which three contained the following herpetofaunal remains: *R. temporaria, Rana* sp. Table 6.16 shows the taxa recovered from each sample.

Table 6.16.

PLL 94 #15 094	*Rana* sp.
PLL 94 #28 198	*R. temporaria, Rana* sp.
PLL 94 #30 248	*R.* cf. *temporaria*

Systematic palaeontology

Rana temporaria

Material. PLL 94 #28 198. One right ilium.

Remarks. This ilium has a ribbed tuber, but the vexillum descends below it. It has been submitted for DNA analysis.

Rana cf. *temporaria*

Material. PLL 94 #30 248. One right coracoid.

Remarks. This matches very closely with modern *R. temporaria*, both in shape and lateral articular surface features.

Rana sp. indet.

Material. PLL 94 #28 198. One femur. #15 094. One partial tibiofibula.

OUTGANG ROAD, MARKET DEEPING, LINCOLNSHIRE

This site is located at Outgang Road in the parish of Market Deeping, Lincolnshire, 12km north-northwest of Peterborough (NGR: TF15871154). It is an infilled oxbow lake, formed by a meander which was cut off from the River Welland during the Iron Age and used as a human settlement during the Iron Age and Roman periods (T. Lane, pers. comm., 1997). Its archaeological significance was recognised during the English Heritage survey in 1986, and the site was excavated by Heritage Lincolnshire in 1991, under the direction of T. Lane. Within an area of 22m x 3m, excavations uncovered the infilled palaeochannel, Iron Age gullies and pits, and Roman ditches and enclosures (Albarella, 1997). The channel fill was mainly organic and contained a large amount of wood and bones. According to archaeological contents, the deposits span the Middle and Late Iron Age to the Roman period (c.2,300-1,600 BP). There appears to have been some reworking of earlier Iron Age material into the overlying Roman contexts, but vertebrate remains came only from the Iron Age levels (Albarella, 1997). The large mammals included cattle, sheep/goat, pig, horse, dog, red deer and beaver. Bones of duck, goose and swan were also recovered and undeterminate rodent remains were noted.

Thirty-four out of fifty-five bags of small vertebrate remains contained herpetofaunal remains. Two bags duplicated the same sample number (MAD 91 #1016 143). The following herpetofaunal list was recovered: *T. cristatus, T.* cf. *vulgaris, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., *N. natrix, Natrix* sp. Table 6.17 lists the samples from which each of the taxa were recovered. Context numbers are given in four digits.

Table 6.17.

MAD 91 #1000 129	*B. bufo, Bufo* sp., Anura indet.
MAD 91 #1002 227	*R. temporaria, Rana* sp., *T.* cf. *vulgaris*
MAD 91 #1003 229	*Bufo* sp., *Rana* sp., Anura indet.
MAD 91 #1004 046	*B. bufo*
MAD 91 #1005 046	*Rana* sp.
MAD 91 #1006 058	*Rana* sp.
MAD 91 #1007	*R. temporaria, Rana* sp., Anura indet.
MAD 91 #1008	Anura indet.
MAD 91 #1009 140	*Rana* sp.
MAD 91 #1013 052	Anura indet.
MAD 91 #1014 082	*Rana* sp., Anura indet.
MAD 91 #1016 143	*Rana* sp., Anura indet., *Natrix* sp.
MAD 91 #1018 238	*Bufo* sp., *Rana* sp.
MAD 91 #1019 268	*Rana* sp.
MAD 91 #1020	*Rana* sp., Anura indet.

MAD 91 #1021	*Bufo* sp.
MAD 91 #1023 321	*Rana* sp., Anura indet.
MAD 91 #1025 371	*Rana* sp., Anura indet., *N. natrix,* Ophidia indet.
MAD 91 #1028	*R. temporaria, Rana* sp.
MAD 91 #1029 433	*T. cristatus*
MAD 91 #1030 354	*R. temporaria, Rana* sp.(brown frog)
MAD 91 #1031 338	*R. temporaria, Rana* sp.
MAD 91 #1032 438	*Bufo* sp.
MAD 91 #1033 463	Anura indet.
MAD 91 #1034	*R. temporaria, Rana* sp., Anura indet., *Natrix* sp.
MAD 91 #1035 600	*Rana* sp., Anura indet.
MAD 91 #1036	*Rana* sp.
MAD 91 #1037	*Rana* sp., Anura indet.
MAD 91 #1039 470	Anura indet.
MAD 91 #1049 683	*Rana* sp., Anura indet.
MAD 91 #1050 679	*Rana* sp.
MAD 91 #1051 547	*Bufo* sp., *Rana* sp.

Systematic palaeontology

Triturus cristatus

Material. MAD 91 #1029 433. One cervical vertebra.

Triturus cf. *vulgaris*

Material. MAD 91 #1002 227. One partial trunk vertebra.

Remarks. The left side of the neural arch and left postzygapophysis is intact, with a flat-topped neural spine.

Bufo bufo

Material. MAD 91 #1004 046. One female metacarpal II. #1000 129. One left ilium.

Bufo sp. indet.

Material. MAD 91 #1051 547. One femur. #1003 229. One partial tibiofibula. #1032 438. One radioulna. #1018 238. One metapodial. #1000 129. One partial right angulosplenial, one coracoid and one metapodial. #1021. One tibiofibula.

Rana temporaria

Material. MAD 91 #1007. One left ilium. #1028. One right ilium. #1031 338. One left

ilium. #1034. One male left humerus. #1002 227. One right ilium.

Remarks. MAD 91 #1031 338. The ilium has a strongly bicostate tuber, a low and depressed vexillum, and a deep pre-acetabular fossa.

Rana cf. *temporaria*

Material. MAD 91 #1030 354. One male right humerus.

Rana sp. indet. (brown frog)

Material. MAD 91 #1030 354. One juvenile left ilium. #1007. One male right humerus.

Remarks. MAD 91 #1007. The lateral crista is not particularly strongly developed, but there is no medial crista at all.

Rana sp. indet.

Material. MAD 91 #1007. Two radioulnae, one left ilial ala, four partial tibiofibulae and two partial femora. #1051 547. One partial tibiofibula, one right scapula and one juvenile left angulosplenial. #1003 229. One partial tibiofibula. #1018 238. One fibulare, one partial tibiofibula and one metatarsal. #1028. One juvenile radioulna. #1007. One trunk vertebra. #1025 371. One partial tibiofibula. #1020. One juvenile femur. #1035 600. One fibulare, two partial tibiofibulae, one juvenile tibiofibula and one partial juvenile femur. #1036. Two right scapulae, two partial tibiofibulae, one partial radioulna and one precoracoid. #1031 338. One femur. #1034. One trunk vertebra and one tibiofibula. #1014 082. One juvenile left angulosplenial. #1002 227. Three partial tibiofibulae, one tibiofibula (in three pieces), and two vertebral fragments. #1009 140. One partial tibiofibula. #1006 058. One partial juvenile femur. #1037. One metatarsal and one left angulosplenial. #1023 321. One tibiofibula. #1050 679. One femur and one left humerus. #1005 046. One atlas vertebra. #1019 268. One partial tibiofibula. #1049 683. One femur. #1016 143. One partial tibiale or fibulare and one partial right maxilla.

Remarks. MAD 91 #1023 321 and #1019 268. The tibiofibulae are distinctly bowed, but probably within the range of a brown frog.

Indeterminate Anura

Material. MAD 91 #1007. One hyoidal cornu, one urostyle, twenty-one partial and fragmentary metapodials and phalanges. #1003 229. One precoracoid. #1000 129. One indeterminate fragment. #1025 371. One urostyle. #1020. One partial femur and one partial metapodial. #1035 600. One radioulna. #1013 052. One partial pterygoid and one metapodial or phalanx. #1039 463. One partial radioulna. #1033 463. One partial urostyle and one juvenile radioulna. #1034. Two phalanges and nine metapodials, phalanges, long bones and fragments thereof. #1014 082. One juvenile left humerus. #1037. Two partial metapodials or phalanges and one partial right humerus. #1023 321. One partial pterygoid, one partial coracoid, one metapodial

or phalanx and one right quadratojugal. #1049 683. One partial metapodial or phalanx. #1008. One phalanx and one partial metapodial or phalanx. #1016 143. Two partial urostyles.

Remarks. MAD 91 #1023 321. The quadratojugal is unusually large.

Natrix natrix

Material. MAD 91 #1025 371. One trunk vertebra.

Remarks. The hypapophysis is broken. The left prezygapophyseal process is intact, angled almost laterally and is therefore *N. natrix.*

Natrix sp. indet.

Material. MAD 91 #1016 143. One trunk vertebra. #1034. One caudal vertebra.

Remarks. MAD 91 #1016 143. The hypapophysis and prezygapophyseal processes are broken.

Ophidia indet.

Material. MAD 91 #1025 371. One partial left rib.

Remarks. This has its distal end missing. Further identification was attempted using the proximal articulation, but although it does not belong to *C. austriaca,* no positive identity could be confirmed.

THIRD DROVE, GOSBERTON, LINCOLNSHIRE

This is a Roman and Early Saxon (c.2,000-1,400 BP) settlement site near the village of Gosberton, 9km north of Spalding in Lincolnshire (NGR TF 17722888). The site was excavated by Heritage Lincolnshire in 1993, under the direction of T. Lane. It consists mainly of infilled ditches, with foraminiferal evidence of a marine influence in Roman times changing to freshwater in Saxon times (T. Lane, pers. comm., 1997). No specific contextual information is known at present.

Nineteen bags of small vertebrate remains have been examined. Five of these produced the following herpetofaunal taxa: *Bufo* sp., *Rana* sp., Anura indet. The taxa found in each sample are listed in Table 6.18.

Table 6.18.

GBT 93 #1 002	*Bufo* sp.
GBT 93 #4 012	*Rana* sp.
GBT 93 #4 016	*Bufo* sp., *Rana* sp., Anura indet.
GBT 93 #20 124	*Rana* sp.
GBT 93 #30 149	*Bufo* sp., *Rana* sp., Anura indet.

Systematic palaeontology

Bufo sp. indet.

Material. GBT 93 #4 016. One left humerus, one left suprascapula, one femur, one radioulna and one trunk vertebra. GBT 93 #30 149. One left humerus. GBT 93 #1 002. One left humerus.

Rana sp. indet.

Material. GBT 93 (Bulk sample) #20 124. One trunk vertebra. GBT 93 #4 016. One radioulna and one tibiale. GBT 93 #30 149. Two femora, one right humerus and one tibiale GBT 93 #4 012. One tibiale or fibulare.

Indeterminate Anura

Material. GBT 93 #4 016. Two radioulnae and three humeri. GBT 93 #30 149. Two phalanges.

MORNINGTON HOUSE, GOSBERTON, LINCOLNSHIRE

This site was a Middle Saxon (c.1,400-1,200 BP) settlement in the parish of Gosberton, 9km north of Spalding in Lincolnshire (NGR TF 17473170). The site was excavated by Heritage Lincolnshire in 1993, under the direction of T. Lane. The digging uncovered a rectangular building surrounded by many ditches (T. Lane, pers. comm.). No other contextual information is known at present.

Bags of small vertebrate remains have been examined from thirty-one samples, of which nine have produced herpetofaunal remains. Sample GOS 93 #17 032 contained fragments of *Mytilus* sp., suggesting proximity to the sea. The following herpetofaunal species were recovered: *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet. The taxa found in each sample are listed in Table 6.19.

Table 6.19.

GOS 93 #1 006	*R. temporaria*
GOS 93 #2 010	*Bufo* sp.
GOS 93 #5 017/19	*Bufo* sp.
GOS 93 #7 018	*Rana* sp., Anura indet.
GOS 93 #9 021	*Bufo* sp., *Rana* sp. (brown frog), *Rana* sp., Anura indet.
GOS 93 #12 022	*Rana* sp.
GOS 93 #30 094	*Rana* sp.
GOS 93 #36 142	*B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
GOS 93 #65 258	*Rana* sp.

Systematic palaeontology

Bufo bufo

Material. GOS 93 #36 142. One sacrum and one right ilium

Bufo sp. indet.

Material. GOS 93 #5 017/019. Tibiofibula fragment. #9 021. One tibiofibula. #7 018. One male right humerus. #36 142. One tibioibula.

Rana temporaria

Material. GOS 93 #36 142. One male right humerus and two right ilia. #1 006. One left ilium.

Remarks. GOS 93 #36 142. These are encrusted with an iron- or manganese-based mineral. The humerus is shown in Figure 6.35c. #1 006. Tuber form is clearly *R. temporaria*, but

the vexillum and part of the ala are missing. One ilium from each sample was submitted for DNA analysis.

Rana sp. indet. (brown frog)

Material. GOS 93 #9 021. One right ilium.

Remarks. This ilium seems to be of an intermediate form between *R. temporaria* and *arvalis* (see Figure 6.35d). The vexillum is relatively high and strongly medially deflected. The tuber is tri-costate, with a depression at its base. There is also a pre-acetabular fossa.

Rana sp. indet.

Material. GOS 93 #65 258. Tibiofibula fragment. #30 094. One tibiale. #9 021. One femur. #7 018. One femur (juvenile). #12 022. One tibiofibula and two tibiofibula fragments. #1 006. One left ilium. #36 142. One tibiofibula and one humerus.

Remarks. GOS 93 #1 006. The ilium was submitted for microsatellite DNA analysis.

Indeterminate Anura

Material. GOS 93 #9 021. One trunk vertebra. #7 018. One right humerus (juvenile). #36 142. One urostyle.

CHOPDIKE DROVE, GOSBERTON, LINCOLNSHIRE

This site was an Early to Middle Saxon (c.1,600-1,200 BP) settlement, in the parish of Gosberton, 9km north of Spalding in Lincolnshire (NGR TF 19882900). It was excavated by Heritage Lincolnshire in 1992, under the direction of T. Lane. It consists of various rectangular structures and ditches, including the foundations of a house. There were also pits which were used for an unknown industrial purpose (T. Lane, pers. comm.). Multidisciplinary environmental work was carried out and is summarised in an interim assessment report by Trimble (1993). Analyses of Foraminifera from the Early Saxon layers revealed an inter-tidal assemblage, characteristic of water depths between 3-5m, with species such as *Elphidium excavatum* forma *clavatum* (M. Godwin in Trimble, 1993). These lower layers are thinly laminated and were interpreted as being marine flood deposits. Later deposits do not contain forams, and the building of a rectangular house during the Middle Saxon period suggests that there was no longer any marine flooding. The transition to freshwater conditions in Middle Saxon times was probably due to silting up of the adjacent fen salt-marshes and estuary (Trimble, pers. comm.).

Four frog bones (samples GOS 92 #52 512, #62 513 and #65 596) were identified by Irving (1995) as *R. lessonae* and indeterminate green frog. These have been re-examined and the identifications are questioned. In addition, bags of small vertebrate remains have been examined from fifty-nine samples, of which thirty-four produced herpetofaunal remains. The full herpetofaunal list recovered is as follows: *T. vulgaris, T.helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, R.* cf. *arvalis/dalmatina, R. lessonae, Rana* sp., Anura indet. The bones identified by Irving (1995) as *R. lessonae* and indeterminate green frog are believed to be *R.* cf. *arvalis/dalmatina* and *Rana* sp. (brown frog) but, ironically, one of the newly identified bones belongs to *R. lessonae*. The location of the sample (GOS 92 #49 133) was in a sill-beam slot, i.e. a foundation trench for the Middle Saxon house (Trimble, pers. comm., 1997). Table 6.20 shows the taxa recovered from each sample.

Table 6.20.

GOS 92 #1 019	*Rana* sp.
GOS 92 #2 024	*T. vulgaris/helveticus, B. bufo, Bufo* sp., *Rana* sp. (brown frog), *Rana* sp.
GOS 92 #6 030	*T. helveticus, B. bufo, Bufo* sp., *Rana* sp.
GOS 92 #8 034	*Rana* sp.
GOS 92 #9 050	*T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., Anura indet.
GOS 92 #11 055	Anura indet.
GOS 92 #12 056	*B. bufo, Bufo* sp., *Rana* sp.
GOS 92 #14 059	*B. bufo, Bufo* sp.
GOS 92 #13 057	Anura indet.
GOS 92 #15 074	*Rana* sp., Anura indet.

GOS 92 #16 065	Anura indet.
GOS 92 #18 078	*B. bufo, Bufo* sp.
GOS 92 #22 099	*Bufo* sp., Anura indet.
GOS 92 #24 101	*Bufo* sp., *Rana* sp.
GOS 92 #26 108	*Bufo* sp., *Rana* sp.
GOS 92 #29 123	*Bufo* sp., Anura indet.
GOS 92 #30 127	*Rana* sp.
GOS 92 #33 204	*Rana* sp.
GOS 92 #38 216	*Rana* sp.
GOS 92 #41 225	Anura indet.
GOS 92 #46 467	*B. bufo, Bufo* sp.
GOS 92 #47 119	*Rana* sp., Anura indet.
GOS 92 #48 089	*R. temporaria, Rana* sp., Anura indet.
GOS 92 #49 133	*B. bufo, Bufo* sp., *R. lessonae, Rana* sp., Anura indet.
GOS 92 #50 279	*T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
GOS 92 #51 280	*Bufo* sp., *Rana* sp., Anura indet.
GOS 92 #52 512	*Bufo* sp., *R.* cf. *arvalis/dalmatina, Rana* sp., Anura indet.
GOS 92 #56 501	*B. bufo*
GOS 92 #57 499	*T. vulgaris, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet.
GOS 92 #59 580	*T. vulgaris/helveticus, B. bufo, Bufo* sp., *Rana* sp., Anura indet.
GOS 92 #62 513	*Bufo* sp., *Rana* sp., Anura indet.
GOS 92 #64 581	Anura indet.
GOS 92 #65 596	*Bufo* sp., *R.* cf. *arvalis/dalmatina, Rana* sp.
GOS 92 #66 646	*B. bufo, Bufo* sp., *Rana* sp., Anura indet.

Systematic palaeontology

Triturus vulgaris

Material. GOS 92 #57 499. One trunk vertebra.

Remarks. The vertebra has a particularly low, flattened neural arch.

Triturus helveticus

Material. GOS 92 #9 050. One trunk vertebra. GOS 92 #6 030. One left prootic-exoccipital.

Remarks. GOS 92 #9 050. The vertebra is elongate, with a fairly pointed neural spine and extensive ventral laminae. #6 030. The prootic-exoccipital is more vertically compressed than in *T. vulgaris* and the overall morphology matches modern *T. helveticus* very closely.

Triturus vulgaris/helveticus

Material. GOS 92 #2 024. One cervical vertebra. #59 580. One cervical vertebra. #9 050. One right frontal. #50 279. One left and one right femur.

Remarks. GOS 92 #9 050. The frontal has its posterolateral process broken, thus the extent of the frontosquamosal arch cannot be seen and specific identification is not possible.

Bufo bufo

Material. GOS 92 #6 030. Two right ilia and one partial right squamosal. #57 499. One sphenethmoid. #14 059. One sacrum. #2 024. One left scapula. #59 580. One right ilium and one partial right ilium. #46 467. One fused sacrum and 8th vertebra. #12 056. One right ilium. #66 646. Two right scapulae. #56 501. One fused sacrum and 8th vertebra. #18 078. One 3rd vertebra. #9 050. One right frontoparietal, two left scapulae, one left and two right ilia. #50 279. Two sacra and one left scapula. #49 133. Two sacra, two left and one right ilia, two left scapulae and one partial right scapula.

Remarks. GOS 92 #18 078. The vertebra was identified using neural spine and cotyle shape. #9 050. One of the right ilia has a very unusual, elongate cristate tuber with two apices.

Bufo sp. indet.

Material. GOS 92 #6 030. One right humerus, one juvenile right scapula, one partial tibiofibula. #57 499. Two trunk vertebrae, one juvenile trunk vertebra, one left humerus, two left and one right partial humeri, one femur, one juvenile right ilial fragment, four partial tibiofibulae, one partial radioulna and juvenile male metacarpal II. #29 123. One partial juvenile tibiofibula. #14 059. One partial trunk vertebra. #2 024. One male left humerus, one right humerus ans one partial right ilium. #24 101. One 3rd vertebra. #65 596. One partial tibiofibula. #52 512. One vertebral fragment and one juvenile trunk vertebra. #59 580. One trunk vertebra, one tibiofibula, one juvenile male metacarpal II and one juvenile partial left humerus. #46 467. One left humerus. #26 108. One male right humerus and one partial trunk vertebra. #12 056. One male right humerus. #66 646. One male right humerus and one right humerus. #22 099. One trunk vertebra and one left humeral shaft. #62 513. One trunk vertebra, one male left humerus and one male right humerus. #18 078. One left angulosplenial. #9 050. Seven trunk vertebrae, one partial right maxilla, one juvenile right scapula, three partial tibiofibulae, one femur, two femoral fragments, one juvenile femur and one juvenile right angulosplenial. #50 279. Two trunk vertebrae, one vertebral fragment, one juvenile tibiofibula, one partial tibiofibula, one juvenile left humerus, one femur and one partial right ilium. #49 133. Three trunk vertebrae, four femora, two partial femora, one left and one right humerus, three left and one right angulosplenials, one partial tibiofibula and one male metacarpal II. #51 280. One femur, one partial tibiofibula and one left humerus.

Remarks. GOS 92 #57 499. The juvenile metacarpal has a clearly visible nuptial crista.

Rana temporaria

Material. GOS 92 #57 499. One left ilium. #48 089. One male left humerus. #50 279. One left and one right frontoparietal.

Rana cf. *arvalis/dalmatina*

Material. GOS 92 #65 596. One left ilium. #62 513.One left ilium.

Remarks. GOS 92 #65 596 was identified as *R. lessonae,* and #62 513 was identified as *Rana* sp. green frog, by Irving (1995). Both identifications are considered incorrect. The ilia have shallow-sloping tubers and thin juncturas, with an angular or sinuous medial edge. They are similar to recent specimens of *R. arvalis* from Sweden (C. Snell collection), but with less bulbous tubers and shallower, more arcuate dorsal vexillum margins. There is no pre-acetabular fossa, but a deep sub-triangular supra-acetabular fossa. The lateral face of the tuber is bulbous lower down, but distinctly flat higher up, tapering into the vexillum. The dorsal acetabular margin is not upstanding cf. green frogs, and certainly not as much as in *R. lessonae.* At present, specific identification is not possible with certainty, owing to the similarity between *R. arvalis* and *R. dalmatina* ilia. The ilium from GOS 92 #65 596 is shown in Figure 6.35e.

Rana sp. indet. (brown frog)

Material. GOS 92 #52 512. One left and one right ilia. #2 024. One juvenile right ilium and one partial juvenile left ilium. #50 279. One partial right frontoparietal, one male left humerus, one male right humerus and one partial left humerus.

Remarks. GOS 92 #52 512. These ilia were identified as *Rana* sp. green frog by Irving (1995), but the identifications are considered incorrect. The left ilium has post-excavation breakage of the tuber and glue obscures some of the diagnostic features of the tuber. It is clearly from a brown frog, probably *R. temporaria.* The tuber appears to be thick, steep, but not high or slender. There is a deep pre-acetabular fossa. The right ilium has shallow ribbing similar ot *R. arvalis,* but it could also belong to *R. temporaria.* The vexillum is broken and its outline cannot be seen. #2 024. These have low tubers but rather continuously high vexillums. They are probably *R. temporaria,* but clearly demonstrate the variability within this species, even in juvenile stages.

Rana lessonae

Material. GOS 92 #49 133. One right ilium.

Remarks. This ilium is shown in Figure 6.36. The vexillum is broken and much of the ala is missing. The tips of the pars ascendens and pars descendens are truncated. The junctura has a fairly straight medial outline, rather than the sinuous outline in brown frogs. There are small undulations in the medial edge of the junctura. These are very comparable to the Thompson Common *R. lessonae* specimen (J. Buckley collection) (Figure 2i in Gleed-Owen and Joslin, 1996), and more pronounced than in any other specimens of green or brown frog. The ventral

acetabular wall is wide, a particular characteristic of green frogs. The d/t ratio is 2.60, which is well within the range of 2.12-2.88 measured for green frogs, and well outside the range of 2.75 -4.00 measured for brown frogs (Gleed-Owen, 1997c). The tuber is well developed and laterally produced. It is intermediate in size and character between that of the Thompson Common and Swedish (C. Snell collection) *R. lessonae* specimens. The tuber is too laterally convex to be *R. ridibunda* or *R. esculenta*. Its form can be considered as at the *R. lessonae* end of the green frog morphological spectrum. There is a deep concavity in the angle between the tuber and the ala. This has not been observed in *R. ridibunda, R. esculenta, R. arvalis* or *R. dalmatina* where instead there is a convex ridge along the vexillum. The tuber is not ribbed and is fairly distinct from any specimens seen of both *R. temporaria* and *R. arvalis*. The acetabular outline is also more rounded, and has a thicker margin than in *R. temporaria*. The dorsal acetabular margin is very upstanding, clearly visible in dorsal view. In *R. temporaria* the dorsal margin is always low, and often depressed so that it is flush with the pars ascendens or even slightly lower than it. In *R. arvalis* and *R. dalmatina* it is slightly higher but certainly lower than in this specimen.

In summary, the combination of a high, robust, laterally produced tuber, a deep concavity between the ala and the tuber, a thick junctura with a low d/t ratio, and an upstanding dorsal acetabular margin, is a firm indication that this specimen belongs to *R. lessonae*.

Rana sp. indet.

Material. GOS 92 #6 030. Two trunk vertebrae, one sacrum and one left angulosplenial. #57 499. Seven trunk vertebrae, one sacrum, one atlas vertebra, one partial left frontoparietal, one male right humerus, one right humerus and three partial tibiofibulae. #33 204. One partial tibiofibula. #2 024. One sacrum, one trunk vertebra, one femur, one partial right frontoparietal and one juvenile left angulosplenial. #24 101. One juvenile right humerus. #65 596. One sacrum and one partial tibiofibula. #47 119. One partial tibiofibula. #52 512. One femur. #59 580. One juvenile trunk vertebra, one sacrum and one partial tibiofibula. #46 089. One female left humerus and one juvenile left scapula. #26 108. One humeral shaft. #12 056. One trunk vertebra, one juvenile sacrum and one juvenile trunk vertebra. #66 646. One trunk vertebra. #38 216. One partial tibiofibula. #62 513. Two trunk vertebrae. #15 074. One right humerus. #1 019. One trunk vertebra and one partial left ilium. #30 127. One trunk vertebra and one juvenile sacrum. #8 034. One juvenile humerus and two juvenile trunk vertebrae. #50 279. Ten trunk vertebrae, eight sacra, two atlas vertebrae, two left humeri, one left angulosplenial, one juvenile right humerus and one metatarsal. #49 133. Two trunk vertebrae, one left squamosal, one sacrum, one left and one right humerus, one juvenile humerus, two femoral fragments and one right angulosplenial. #51 280. One trunk vertebra, two partial femora, one male left humerus and one partial humerus.

Remarks. GOS 92 #51 280. The partial humerus has a sharp, splintered break on the shaft.

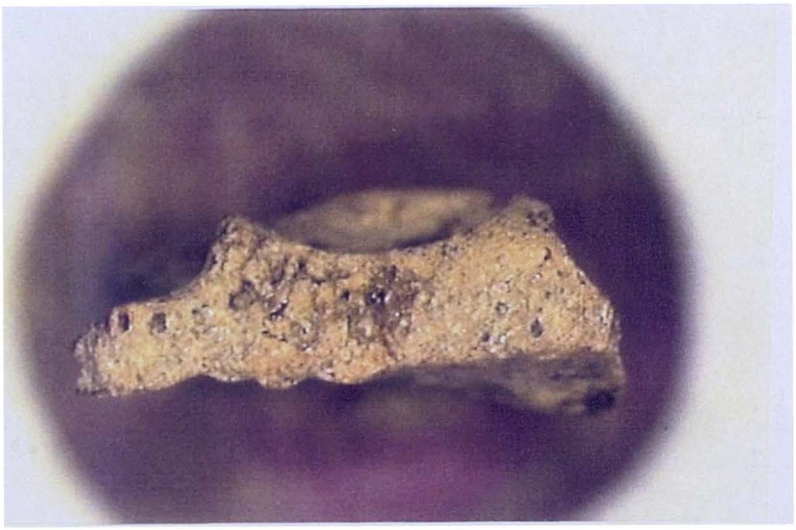


Figure 6.36: Right ilium of *R. lessonae* from Gosberton Chopdike Drove, Lincolnshire (sample GOS 92 #49 133): a) left lateral view; b) junctura ilioischiadica (posterior view); c) dorsal view.

Indeterminate Anura

Material. GOS 92 #6 030. One partial sacrum, seven vertebral fragments, one juvenile radioulna, one juvenile left scapula, three phalanges, one male metacarpal fragment, one partial left humerus, one juvenile left humerus and one partial exoccipital. #57 499. One 3rd vertebra, one left and one right exoccipital, one humerus, four partial humeri, one radioulna, two vertebral fragments, one urostyle, one ischium and one phalanx. #29 123. One juvenile humerus. #41 225. One juvenile radioulna. #47 119. One partial urostyle. #64 581. One partial trunk vertebra. #52 512. Two left exoccipitals and one partial trunk vertebra. #59 580. One sacrum, one partial atlas vertebra, one ischium, one left exoccipital, one partial sacrum and three vertebral fragments. #46 089. One left and one right exoccipital and one ischium. #66 646. Two vertebral fragments. #22 099. One partial urostyle, one juvenile humeral fragment and one vertebral fragment. #62 513. One right exoccipital, one ischium and one juvenile humerus. #15 074. One right exoccipital and one right humerus. #16 065. One ischium. #11 055. One prootic and one exoccipital. #9 050. Four vertebral fragments, one right exoccipital, one partial urostyle, one partial metapodial and one phalanx. #50 279. Twenty-five vertebral fragments, one coracoid, one precoracoid, one partial urostyle, one ischium, one juvenile humerus, two partial radioulnae, one prootic, one left exoccipital, one pterygoid and two sphenethmoids. #49 133. Two right exoccipitals, seven vertebral fragments, three urostyles, five radioulnae, three coracoids, six phalanges and long bone fragments, one juvenile humerus, one partial left angulosplenial and one partial precoracoid. #13 057. One partial sacrum. #51 128. One humeral shaft, one radioulna and one long bone fragment.

HAY GREEN, TERRINGTON ST. CLEMENT, NORFOLK

This is a Middle and Late Saxon (c.1,400-1,000 BP) occupation site in the parish of Terrington St. Clement, 8km west of King's Lynn in Norfolk. Two sites within the area were excavated in 1992 by the Norfolk Archaeological Unit, under the direction of A. Crowson: Site 22275 (NGR TF 537182) and Site 22276 (NGR TF 541176). These have not been published, but a summary was given for Hay Green by Leah and Crowson in Gurney (1993). Scattered Ipswich Ware pottery found during fieldwork had demonstrated that the Middle Saxon site extends for c.1.5km along a 'roddon', and is the largest site of this age in Marshland. Two trenches across the roddon revealed a number of substantial silt-filled ditches running across it. Foraminiferal analysis showed that the silts were deposited under active marine conditions. A number of pits with charcoal-rich fills were also sectioned and contain evidence of salt-tolerant crop production. Late Saxon features did not contain marine silts, apparently due to the construction of a 'seabank' (Leah and Crowson in Gurney, 1993).

One frog ilium (sample 22275 TSC #3 022) was identified as *Rana* sp. green frog by Irving (1995). This has been re-examined and the identification is questioned. A further nineteen bags of small vertebrate remains have been examined, of which four produced herpetofaunal remains. The herpetofaunal assemblage recovered is as follows: *Bufo* sp., *R.* cf. *arvalis*, *Rana* sp., Anura indet. The taxa found in each sample are listed in Table 6.21.

Table 6.21.

22275 TSC #3 022	*R.* cf. *arvalis*
22275 TSC #4 075	*Bufo* sp., Anura indet.
22276 TSC #1 030	Anura indet.
22276 TSC #3 106	*Rana* sp., Anura indet.

Systematic palaeontology

Bufo sp. indet.

Material. 22275 TSC #4 075. One femur (pathological).

Remarks. The femur is incomplete. One end is swollen, but there is a strongly developed crista along the undamaged part of the shaft.

Rana cf. *arvalis*

Material. 22275 TSC #3 022. One left ilium.

Remarks. See Figure 6.35f. The vexillum is broken but appears to have been relatively high. The tuber has a fairly shouldered apex which is slightly curved medially. It is relatively steep and is unlikely to belong to *R. dalmatina*. Its lateral face is slightly ribbed cf. *R. arvalis*. It is not as

laterally produced as *R. temporaria* and has much weaker ribbing. The dorsal acetabular margin is depressed. The junctura is thin, with a sinuous medial edge. There is no pre-acetabular fossa.

Rana sp. indet.

Material. 22276 TSC #3 106. Three partial tibiofibulae and one right scapula (juveniles) and one sacrum. 22275 TSC #4 075. One femur.

Indeterminate Anura

Material. 22276 TSC #1 030. One partial radioulna. 22276 TSC #3 106. One coracoid and two humeri (juvenile).

INGLEBOROUGH FARM, WEST WALTON, NORFOLK

This is a Middle to Late Saxon site (c.1,400-1000 BP), near the village of West Walton, 4km north of Wisbech in Norfolk (NGR TF 47271481). Norfolk Archaeological Unit excavated it in 1992 (site code 18943) under the direction of A. Crowson. A final publication has not been produced but a summary was given by Leah and Crowson in Gurney (1993). A scatter of Ipswich Ware and local pottery was centred on a low rise c.100m in diameter. Excavation showed that this was the highest part of a roddon which had largely been buried by post-Roman silt. A number of substantial silt-filled ditches, of probable Middle Saxon age, were cut into the roddon. In contrast, a number of Late Saxon features found were not silt-filled. This was interpreted as being the result of the construction of the seabank found immediately to the north of the site (Leah and Crowson in Gurney, 1993).

Twenty-eight bags of small vertebrate remains have been examined for herpetofaunal remains, of which ten contained herpetofaunal remains. Four of the bags were from only two samples, thus eight samples are represented by herpetofaunal remains. The following herpetofaunal taxa were identified: *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet. The species recovered from each sample are listed in Table 6.22.

Table 6.22.

18943 WNW #2 063	*Bufo* sp.
18943 WNW #4 069	*Bufo* sp.
18943 WNW #8 088	Anura indet.
18943 WNW #11 095	*Rana* sp.
18943 WNW #13 104	*B. bufo, Bufo* sp., *Rana* sp., Anura indet.
18943 WNW #15 110	Anura indet.
18943 WNW #17 115	*R. temporaria*, Anura indet.
18943 WNW #19 186	*Rana* sp. (brown frog), *Rana* sp., Anura indet.

Systematic palaeontology

Bufo bufo

Material. 18943 WNW #13 104. One right ilium and one partial left squamosal.

Remarks. This ilium has been submitted for microsatellite DNA analysis.

Bufo sp. indet.

Material. 18943 WNW #2 063. One left humerus. #13 104. One right humerus and two associated trunk vertebrae. #4 069. Two right humeri. #2 063. One right angulosplenial and one right maxilla.

Remarks. 18943 WNW #4 069. One right humerus is stained a deep bluish grey.

Rana temporaria

Material. 18943 WNW #17 115. One left ilial ala.

Remarks. This has a continuously low, medially curled vexillum, characteristic of only *R. temporaria*. The specimen has been submitted for DNA analysis.

Rana sp. indet. (brown frog)

Material. 18943 WNW #19 186. One partial right ilium.

Remarks. The corpus is missing, but the tuber is very thin, with only fine ribbing. The vexillum is higher than the tuber suggesting *R. arvalis*, but the tuber and part of the vexillum are strongly folded laterally, and the middle section of the vexillum is strongly medially deflected.

Rana sp. indet.

Material. 18943 WNW #11 095. Two trunk vertebrae and one partial left frontoparietal (parietal part). #13 104. One third trunk vertebra fragment. #19 186. One left scapula and one left angulosplenial (both juvenile).

Indeterminate Anura

Material. 18943 WNW #17 115. One right exoccipital. #8 088. One radioulna fragment. #19 186. One left and right humerus, one partial femur, six partial tibiofibulae, one right scapula, one partial trunk vertebra and two metapodials or phalanges (all juvenile). #13 104. One vertebral fragment and two phalanges. #15 110. One phalanx.

ROSE HALL FARM, WALPOLE ST. ANDREW, NORFOLK

This site is located in the parish of Walpole St. Andrew to the east of the River Nene, 10km north-northeast of Wisbech in Norfolk (NGR TF 48741600). This is a Middle Saxon (c.1,400-1,200 BP) occupation site. It was excavated in 1992 by Norfolk Archaeological Unit (site code 22145), under the direction of A. Crowson. The site is not published but a summary was given by Leah and Crowson in Gurney (1993). The site was identified by a scatter of Ipswich Ware for c.800m along a roddon. A trench was cut across the site, revealing silt-filled ditches. These contained Foraminifera and the silts were deposited under an active marine influence.

Twenty-four bags of small vertebrate remains have been examined, of which four contained herpetofaunal remains. The following sparse herpetofaunal assemblage was identified: *Rana* sp., Anura indet.. The taxa recovered from each sample are listed in Table 6.23.

Table 6.23.

22145 WPA #5 216	*Rana* sp., Anura indet.
22145 WPA #6 207	Anura indet.
22145 WPA #10 231	*Rana* sp.
22145 WPA #12 017	*Rana* sp.

Systematic palaeontology

Rana sp. indet.

Material. 22145 WPA #10 231. One sacrum. #12 017. One partial juvenile left scapula. #5 216. One sphenethmoid.

Indeterminate Anura

Material. 22145 WPA #5 216. One partial exoccipital. #6 207. One partial humeral shaft.

DEEPING ST. JAMES, LINCOLNSHIRE

This site is a working commercial gravel pit (NGR TF185081), situated adjacent to the north bank of the River Welland which marks the boundary with Cambridgeshire to the south. Merry (1995) discussed various aspects of the site's stratigraphy and faunal character, particularly the molluscan assemblage. The site lies under the first terrace of the Welland, with Devensian (and later Stage 5?) fluviatile gravels overlying interglacial organic deposits which are interbedded within them towards their base (see Figure 6.37). The interglacial units comprise organic lenses and richly fossiliferous organic silt channel infills (Merry, 1995). A diverse range of Mollusca, Coleoptera, Ostracoda, pollen, plant macrofossils and vertebrate remains have been identified by a multidisciplinary team, and publication is expected in 1998.

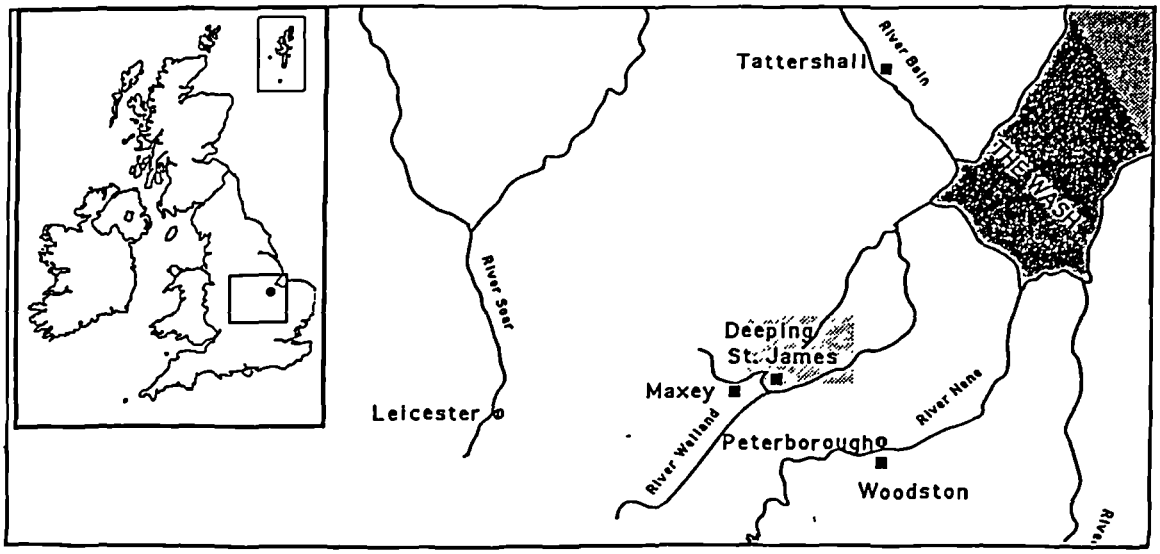
The molluscan assemblage is dominated by a preponderance of the thermophile *Belgrandia marginata* (Merry, 1995, pers. comm.; D.H. Keen, pers. comm., 1997). Several species from the assemblage, including *Cochlicopa nitens*, are absent from Britain today, and the fauna indicates a warmer, drier, more continental climate than today's (Merry, 1995). G.R. Coope (pers. comm. to Merry, 1995) identified an assemblage of 200 beetle taxa. Fifteen taxa are now extinct in Britain, most of which are now confined to central and southern Europe today, although *Heptaulacus* sp. is not found in Europe. The ostracod fauna includes *Candona fabaeformis* which is absent from Britain today (Merry, 1995). Plant macrofossil data indicate a Last Interglacial age (M.H. Field, pers. comm., 1997), and palynological spectra place the deposits at zone Ip IIb (T. Mighall, pers. comm., 1997). A partly-associated skeleton of a juvenile straight-tusked elephant was also recovered, along with numerous other bones of this species and *Bos* sp. (D.H. Keen, pers. comm., 1998). Absolute dating by TL and OSL gave ages of c.115-122 kA BP (M. Bateman, pers. comm. to D.H. Keen, 1997). The collective evidence strongly indicates an Ipswichian age for the interglacial deposits, and suggests a climate at least 2-3°C warmer than today (Merry, 1995).

Samples taken by J. Merry between 1994 and 1996, which were scanned for Mollusca, produced a few small vertebrate remains (Merry, 1995). These have been examined and the following herpetofaunal taxa identified: *B. bufo, Rana* sp., *N.* cf. *maura/tessellata, Natrix* sp. The taxa identified from each sample are listed in Table 6.24. The material is currently in the possession of J. Merry (COV). The '*Natrix* sp.' trunk vertebra cannot be located at present, and the identification should be regarded as undeterminate rather than indeterminate.

Table 6.24.

'DSJ Bulk sand lens 24/9/96'	*B. bufo, N.* cf. *maura/tessellata*
'Deeping St. James'	*Rana* sp.
Unspecified sample	*Natrix* sp. (undeterminate)

a)



b)

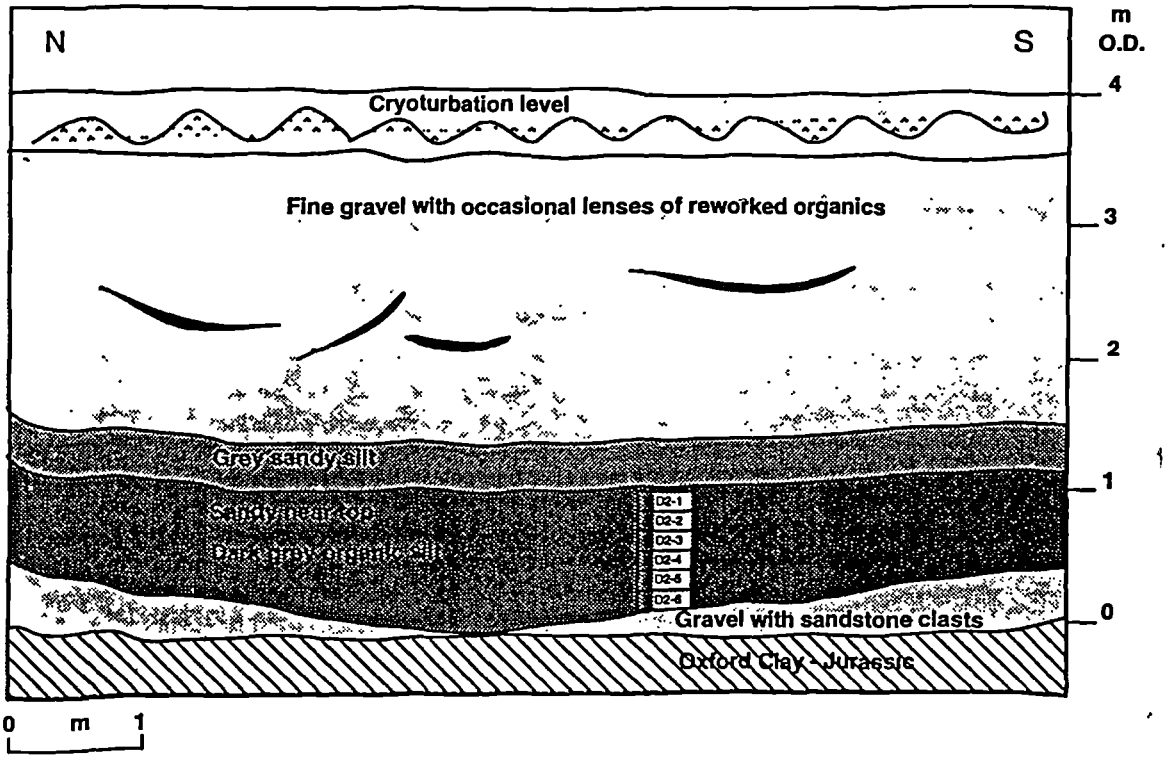


Figure 6.37: Deeping St. James, Lincolnshire: a) Location; b) Schematic section through Late Pleistocene deposits (after Merry, 1995).

Systematic palaeontology

Bufo bufo

Material. DSJ Bulk sand lens 24/9/96. One right scapula (in two pieces).

Remarks. There is a small foramen adjacent to the glenoid margin, much smaller than the fossa which is characteristic of *B. calamita*.

Rana sp. indet.

Material. "Deeping St. James". One radioulna.

Remarks. This is thinner than in *Bufo*, with a narrower articular end. The lateral foramen is small and inconspicuous compared to *Bufo* in which it can be seen from above.

Natrix cf. *maura/tessellata*

Material. DSJ Bulk sand lens 24/9/96. One caudal vertebra.

Remarks. The neural spine is missing, but the high neural arch is natricine. There are a pair of parallel, broken haemapophyses. One parapophyseal process (left side intact) is angled anterolaterally rather than laterally, and extends beyond the prezygapophysis.

Natrix sp. undet.

Material. Unspecified sample. One trunk vertebra.

Remarks. This specimen cannot be located at present, and re-examination has not been possible since the initial identification during 1996.

6.5 Northern England

CRESWELL CRAGS, CRESWELL, DERBYSHIRE

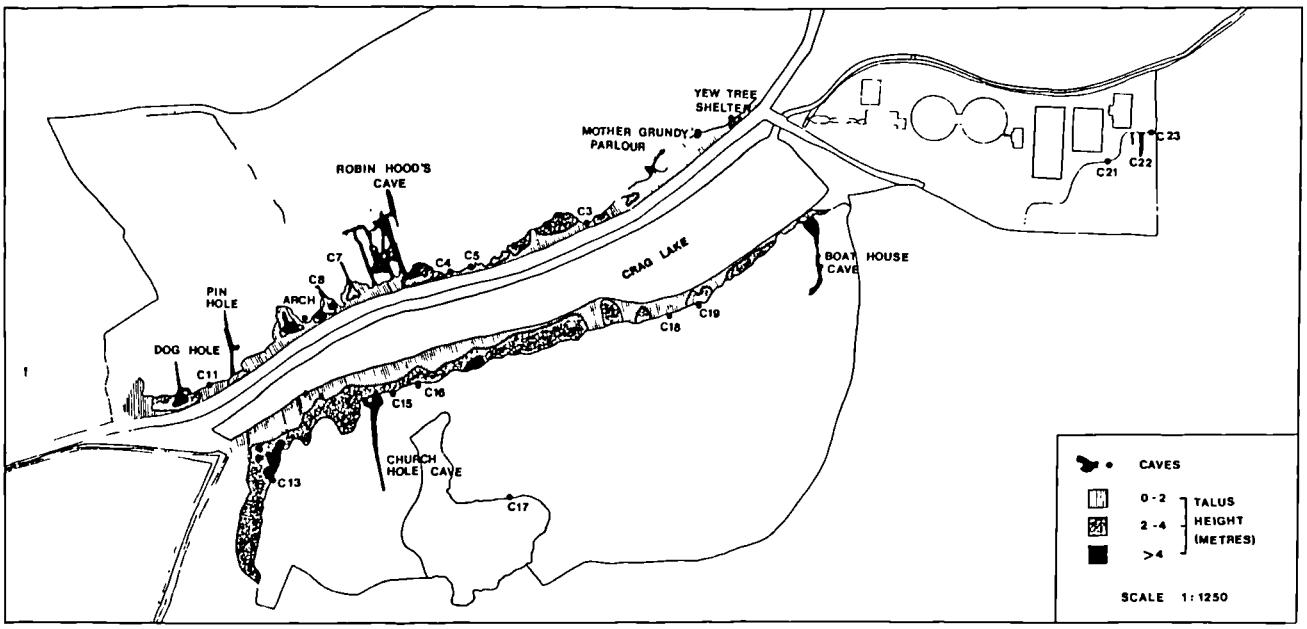
Creswell Crags is a gorge situated to the east of the village of Creswell, at the northeast corner of Derbyshire. The surrounding topography is a low and undulating range of hills rising from a plateau of Lower Permian Magnesian Limestone. The gorge is about 500m long, oriented WSW to ENE (see Figure 6.38a) and about 70m wide. Its wooded sides form steep cliffs about 10-20m high. The gorge contains a number of caves, well known since the mid-19th Century for their Late Pleistocene and Holocene mammalian assemblages, and their Upper Palaeolithic and Mesolithic archaeology. Twenty-three caves are now known, eight of which are named. The flat floor of the gorge contains the long, narrow Crag Lake created by deliberate damming of the western end and flooding of the gorge floor during the 19th Century (Jenkinson and Gilbertson, 1984). .

An account of the history of work on the caves was given by Jenkinson (1984) and Jenkinson and Gilbertson (1984). Early excavations were carried out at Pin Hole Cave, Church Hole Cave and Robin Hood's Cave, by T. Heath, M. Mello, and W. Boyd Dawkins in the 1870's (Dawkins, 1876). Although an abundance of large mammal remains were recovered, this work was poorly recorded and collaboration between excavators ended acrimoniously. Various phases of uncontrolled excavation, sometimes with explosives, persisted into the 1880's. R. Laing subsequently worked in Dog Hole Cave and Robin Hood's Cave, and W. Duckworth and F. Swainson later worked on the un-named Cave 8. After a period of little interest in the caves, work resumed in the 1920's when A. Armstrong commenced work in the gorge. He carried out a series of excavations between 1930 and 1950, in Mother Grundy's Parlour and Pin Hole Cave. The quality of these excavations surpassed all previous work and, for the first time, sediments were sieved for small vertebrate and other faunal remains. Armstrong also found that Pin Hole Cave contained additional sediments which had been missed by Dawkins in 1875. After Armstrong's death, C. McBurney continued work at Mother Grundy's Parlour in 1959 but these excavations have not been published. Further work at Mother Grundy's Parlour and Robin Hood's Cave was conducted by J. Campbell during the late 1960's (Campbell, 1969). This gave rise to the recognition of earlier and later phases in Upper Palaeolithic Archaeology, and the concept of the Cresswellian (Campbell, 1977). Smaller excavations by S. Collcutt have also been undertaken at Mother Grundy's Parlour, Robin Hood's Cave and Dog Hole Cave (Collcutt, 1975). Accounts of recent work in the gorge and its caves are given in Jenkinson and Gilbertson (1984).

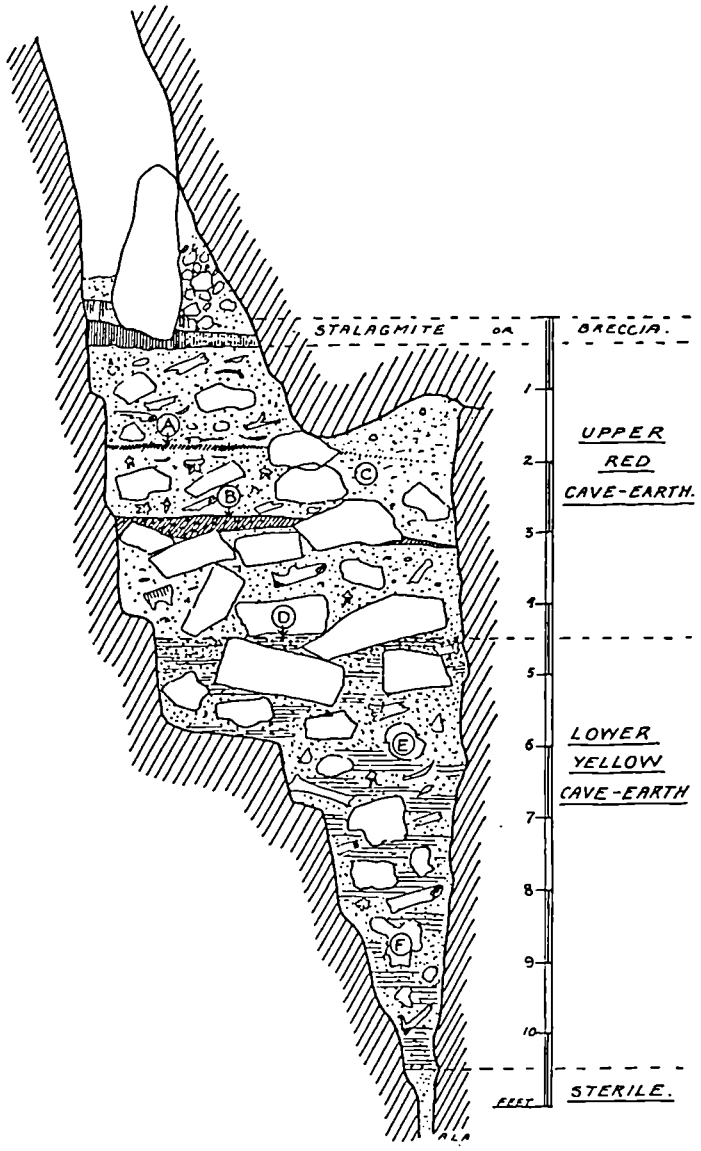
No herpetofaunal material has previously been specifically identified from the caves, though its presence has been noted. *Rana* sp. was recorded from Holocene sediments in Dog Hole Fissure, along with a typical Holocene vertebrate assemblage including horse, red deer, fox, beaver, wood mouse, bats and salmon (Briggs *et al*, 1984). Bulked bone fragments of wolf, red deer and wild boar from Mesolithic sediments gave an age of 9,960±140 ^{14}C BP (HAR 4309).

Rana sp. and Lacertidae sp. were also recorded from sediments at Steetley Cave during 1981

a)



b)



June, 1925.
A and B—Black bands and hearths. C—The rodent corner.
D—Upper Mousterian level. E—Lower Mousterian level.
F—Lower Palæolithic level.

Figure 6.38: a) Plan of Creswell Gorge, Derbyshire, and its caves (after Jenkinson and Gilbertson, 1984); b) Schematic lithostratigraphic section of Pleistocene and Holocene deposits in Pin Hole Cave, Derbyshire, as exposed in 1925 excavations (after Armstrong, 1929).

(Bramwell *et al*, 1984). The associated Mesolithic archaeology, palynology and large mammals (including lynx, wildcat, roe deer, sheep and cow) indicate a wooded local environment during the early to middle Holocene. The large proportion (c.30%) of anuran remains were interpreted as being an assemblage accumulated by badger, lynx and wildcat.

The nature of early excavations and problems in the curation of remains has meant that much of the vertebrate material was irretrievably mixed and could not usefully be studied. Recent excavations have been more controlled and will hopefully produce material from a range of age contexts in future. A few preliminary samples from Pin Hole Cave and Robin Hood's Cave have been studied. The material is held in the research collection of the Cresswell Crags Visitor Centre, and is now under the curation of Brian Chambers and Ian Wall.

PIN HOLE CAVE

This is a small cave located in the northern outcrop of the Creswell Gorge, towards its western end (NGR SK533742). Mello (1875) first recorded the cave as 'Fissure A'. The numerous vertebrate remains he recovered included cave hyaena, wolf, fox, arctic fox, glutton, brown bear, mammoth, woolly rhinoceros, reindeer, giant deer, aurochs, sheep, horse, brown hare and indeterminate voles (Mello, 1875; Jenkinson, 1984). Mello (1875) also noted that most of the archaeology he found was Neolithic and situated near to the surface of his excavations.

The cave was later systematically excavated by Armstrong (1929) who gave a clear account of the stratigraphy encountered (see Figure 6.38b) and the associated stone tool 'industries'. The cave extends for some 60m, with a narrow column of sediment often over 4m in depth extending for much of this length (Armstrong, 1929). He described an upper sandy humus, with 75cm of reddish brown 'Upper Cave-earth' beneath. It contained Upper Palaeolithic stone tools of Aurignacian and Creswellian type, and a large mammal fauna with mammoth, woolly rhinoceros, arctic fox and hare. Mousterian artefacts at the base marked the clear junction with the yellow 'Lower Cave-earth', with a typical Middle Devensian large mammal assemblage including reindeer, mammoth, woolly rhinoceros, wolf and hyaena. Towards the base of this unit (3-3.5m depth from the surface), fragments of mammoth tusk were found in association with crude Acheulian implements. These basal sediments are likely to be Middle Pleistocene in age.

Jenkinson and Bramwell (1984) provided an account of Pin Hole Cave's archaeology and palaeontology, though their revised stratigraphic division of sediments is not entirely clear. According to Jenkinson and Bramwell, the sediments span from the Early Devensian to the Holocene and may go back further. Middle Palaeolithic archeology dates Levels 8-13 to the Middle Devensian, and a piece of reindeer antler from Level 12 was radiocarbon dated to c.39ka BP. Early Upper Palaeolithic archaeology from higher levels probably dates to c.30ka BP, and a late Upper Palaeolithic backed blade industry from Levels 1-4 indicates deposition no earlier than 10ka BP.

A large number of bird remains were recovered by Armstrong (1929), but were only fully described by Jenkinson and Bramwell (1984). The avifauna includes black throated diver, brent

goose, barnacle goose, ptarmigan, red grouse, blackbird, demoiselle crane, white stork, golden eagle, buzzard, osprey and large numbers of kestrel. Some of the fifty species were present throughout the Middle and Late Devensian, and the avifauna was particularly diverse during a period believed to correlate with the Upton Warren Interstadial Complex (Jenkinson and Bramwell, 1984). Only a few species were present during the glacial maximum, but species diversity increased during the Lateglacial period with the colonisation of arboreal species among others.

Four tubs of sorted bone from Pin Hole Cave were examined for herpetofaunal remains in May 1996. Three were labelled 'Armstrong spoil', and were sampled from spoil discarded in Armstrong's excavations. As these samples are of unknown context they are of little biostratigraphic use. A tub of sorted remains labelled 'PH 1995' was also studied (non-specifically identifiable elements were not removed), but the context of this sample is also unknown. The deposits excavated by Armstrong may have spanned a range of 6-700,000 years (R. Jacobi, pers. comm.). However, most of the material excavated was of Devensian and Holocene age, and in association with the large mammal fauna detailed above. It is most likely, however, that the herpetofaunal remains are of Holocene age.

The remains are held in the Creswell Crags Visitor Centre collection. The herpetofaunal list is as follows: *T.* cf. *vulgaris*, *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet. Table 6.25 shows the taxa recovered from each of the two samples.

Table 6.25.

Armstrong spoil	*T.* cf. *vulgaris*, *B. bufo, R. temporaria, Rana* sp., Anura indet.
PH 1995	*B. bufo, Bufo* sp., *R. temporaria.*

Systematic palaeontology

Triturus cf. *vulgaris*

Material. 'Armstrong spoil'. One trunk vertebra.

Remarks. The vertebra has a broad, shouldered posterior neural arch.

Bufo bufo

Material. 'Armstrong spoil'. One partial sacrum and one right maxilla. PH 1995. One right frontoparietal, one sacrum and one tibiofibula.

Bufo sp. indet.

Material. PH 1995. One left premaxilla, one left maxilla, one phalanx, two suprascapulae, one sacrum, two left humeri, one partial metacarpal and three male second digit metacarpals.

Rana temporaria

Material. 'Armstrong spoil'. Two left and one right frontoparietal, six left and eight right ilia and two male second digit metacarpals. PH 1995. Ten left and six right ilia, one left and one right frontoparietal.

Rana sp. indet.

Material. 'Armstrong spoil'. Two partial scapulae, one omosternum, one coracoid, one ilial ala, one urostyle and other elements.

Indeterminate Anura

Material. 'Armstrong spoil'. Indeterminate fragments.

ROBIN HOOD'S CAVE

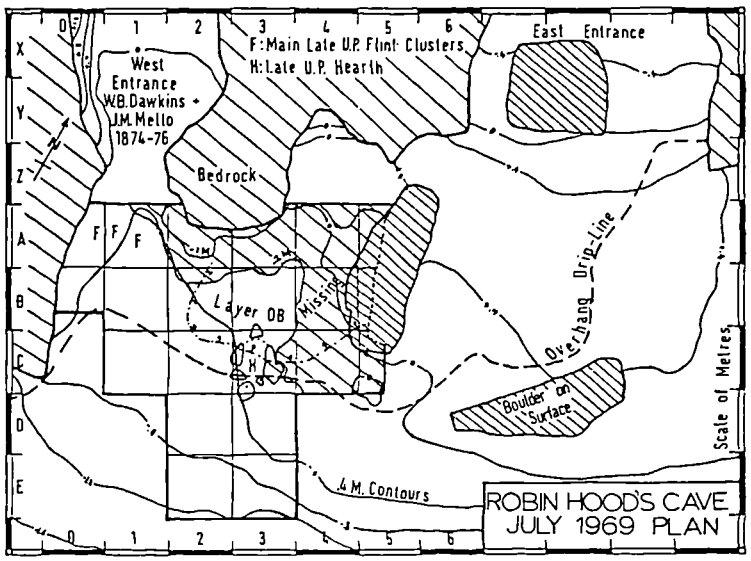
This cave (NGR SK534742) is one of the largest systems in the Creswell gorge, consisting of at least four large chambers and a number of inter-connected passages (Jenkinson and Bramwell, 1984). Much of the cave was excavated during the 19th Century (e.g. Mello, 1875), but Campbell (1969) carried out further digging in the western talus area (see Figure 6.39). Vertebrate remains were recorded by Dawkins (1876; 1877) and re-examined by Jenkinson (1984). Like Pin Hole Cave, they demonstrate a typical Middle Devensian cold-stage assemblage dominated by cave hyaena, cave lion, brown bear, wolf, bison, mammoth, woolly rhinoceros, reindeer, horse and giant deer.

Seventeen species of bird recovered from the Campbell excavations were identified by D. Bramwell, including mallard duck, ptarmigan, black grouse, grey plover, magpie, jackdaw, kestrel and goshawk (Jenkinson, 1984; Jenkinson and Bramwell, 1984). Overall, the mammal and bird faunas of Pin Hole Cave and Robin Hood's Cave are very comparable. The mammal fauna from what Dawkins (1977) described as a 'superficial layer' included wildcat, dog, fox, pine marten, stoat, badger, red deer, roe deer, sheep/goat, pig and hare. This is clearly a Holocene assemblage.

Dawkins (1877) also recorded a rich archaeological assemblage from Robin Hood's Cave, with over 1,000 implements. The oldest were quartzite choppers, with a later preponderance of lanceolate flint blades as well as worked bone and antler. The most important single artefact was a piece of rib engraved with the head of a horse. Most of the Late Palaeolithic flint implements are from the 'breccia' whereas the hyaena-dominated fauna came from the underlying 'cave-earth' (Dawkins, 1877). Campbell (1969) described the flint archaeology of Robin Hood's Cave in detail, initiating the 'Creswellian' terminology for the Late Upper Palaeolithic. A rise in sub -triangular backed blades was associated with abundant reindeer, wild horse, woolly rhinoceros and hyaena (Campbell, 1969).

A small number of anuran bones from Robin Hood's Cave was examined in December 1996. These were picked from six samples from the 'Horseshoe Passage' and provided by R. Jacobi. Sample numbers are those used by Jacobi. The deposits are of Holocene age, based on faunal and stratigraphic evidence, and the only associated large mammal material was a small fragment of wildcat bone (Jacobi, pers. comm., 1997). These remains form only a preliminary investigation into the herpetofauna of Robin Hood's Cave. Additional samples are being sorted and it is expected that further material will become available for study in the near future. The material studied is presently in the possession of R. Jacobi (NHM). The total herpetofaunal list is: *B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet. Table 6.26 shows the taxa recovered from each sample.

a)



b)

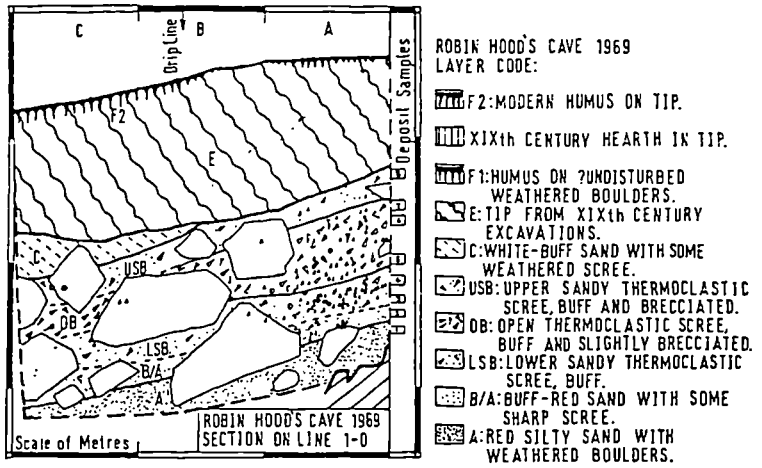


FIG. 3. Robin Hood's Cave, section on line 1 - 0.

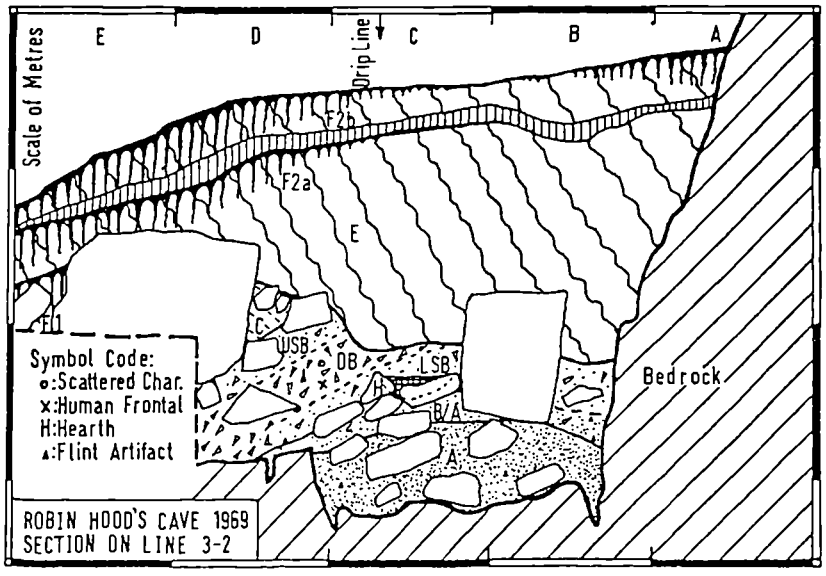


Figure 6.39: Robin Hood's Cave, Derbyshire: a) Plan of main chamber and excavated areas; b) Lithostratigraphic sections of Pleistocene and Holocene deposits (after Campbell, 1969).

Table 6.26.

RH-1763, RH-7C3	*B. bufo, Bufo* sp., Anura indet.
RH-1767, RH-7C10	*Rana* sp., Anura indet.
RH-1770, RH-7C4	*Bufo* sp., *R. temporaria, Rana* sp.
RH-1781, AEA-7C5	*B. bufo*, Anura indet.
RH-1782, AEA-7C15	*B. bufo, Bufo* sp., *Rana* sp., Anura indet.
RH-1784, AEA-7C14	*Bufo* sp., Anura indet.

Systematic palaeontology

Bufo bufo

Material. RH-1781, AEA-7C5. One right ilium. RH-1782, AEA-7C15. One right ilium and two left scapulae. RH-1763, RH-7C3. One sacrum.

Bufo sp. indet.

Material. RH-1782, AEA-7C15. Two left humeri and one left radioulna. RH-1784, AEA-7C14. One male right humerus. RH-1763, RH-7C3. One coracoid and one urostyle. RH-1770, RH 7C4. One right humerus.

Rana temporaria

Material. RH-1770, RH 7C4. One ilial ala fragment.

Rana sp. indet.

Material. RH-1782, AEA-7C15. One female left humerus. RH-1767, RH 7C10. One right coracoid. RH-1770, RH 7C4. One left scapula and one fragmentary trunk vertebrae.

Indeterminate Anura

Material. RH-1781, AEA-7C5. One metapodial or phalanx. RH-1782, AEA-7C15. One phalanx and one right angulosplenial. RH-1784, AEA-7C14. One angulosplenial and one fragmentary scapula. RH-1763, RH-7C3. Several indeterminate fragments. RH-1767, RH-7C10. One left pterygoid.

WHITEMOOR CHANNEL, BOSLEY, CHESHIRE

This site, situated near Bosley in east Cheshire (NGR SJ917678), is a glacial meltwater channel scoured between 22-15,000 ka BP (Johnson *et al*, 1970). A depression in the centre of the channel forms an elongate trough and is infilled with Late Pleistocene and Holocene alluvial sediments (see Figure 6.40). Johnson *et al* (1970) cored the infill in the centre of the depression and recorded the following stratigraphy:

0.00-1.65m	Fen peat
1.65-1.95m	White calcareous marl
1.95-2.10m	Blue-grey calcareous mud
2.10-9.00m+	Blue-grey silty clay (bottom not reached)

The stratigraphy and pollen spectra show that the sediments span the Lateglacial and Holocene (Johnson *et al*, 1970). The marl produced a sparse, slum molluscan fauna of *Lymnaea peregra, Gyraulis albus* and *Sphaerium corneum*, five ostracod species and abundant *Chara* indicating a stagnant pond with alkaline conditions (pH 7 or 8). The pollen from this layer demonstrate the development and persistence of a closed birch woodland and date it to Pollen Zone V, c.8,000-7,200 BP (Johnson *et al*, 1970).

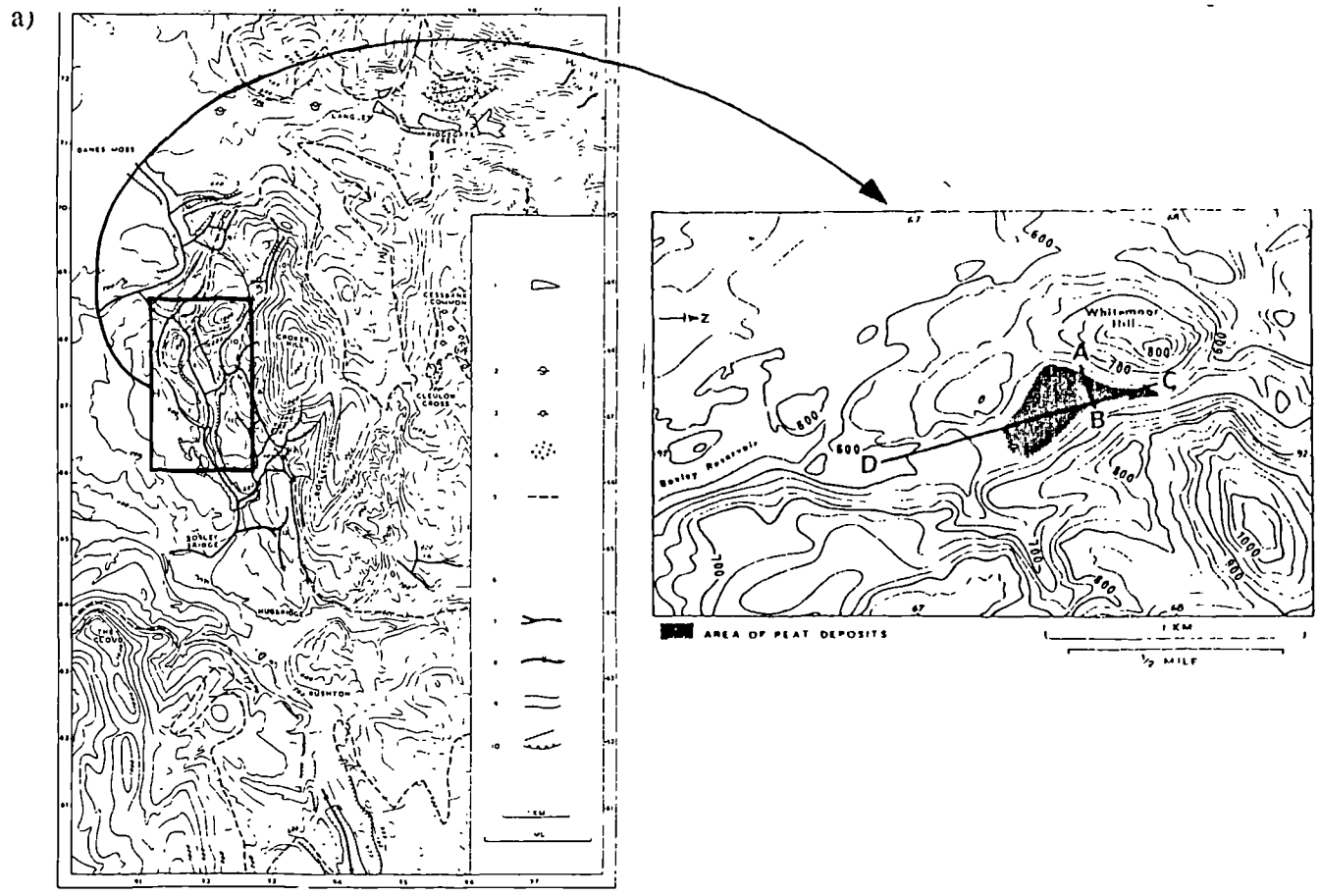
A.J. Stuart reported amphibian remains from the marl as *Triturus* sp., *B. bufo* and *R. temporaria* (Stuart in Johnson *et al*, 1970; Stuart, 1974). Holman and Stuart (1991) later described the amphibian fauna in detail and listed *T. vulgaris, T. helveticus, B. bufo, B. calamita* and *R. temporaria*. The record of *B. calamita* was based on two left ilia and a sacrum. In the light of the current project, it was decided that the material should be re-examined, largely because the figure given by Holman and Stuart (1991) appeared to be of *B. bufo*, rather than *B. calamita* as reported. Using the characters described in Chapter 5, it is apparent that the ilia and sacrum belong to *B. bufo* as originally identified by Stuart (in Johnson *et al*, 1970; Stuart, 1974). Furthermore, the scapulae identified as *Bufo* sp. (Holman and Stuart, 1991) all belong to *B. bufo*. The material is held at the Norwich Castle Museum.

Systematic palaeontology

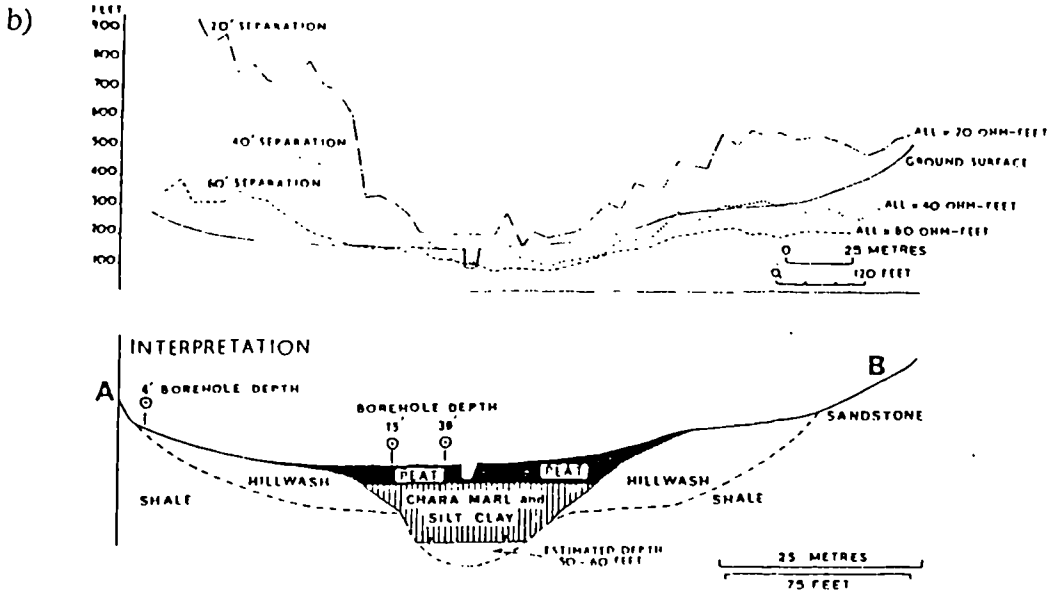
Bufo bufo

Material. NCM 143.949, WC 96-98. Two left ilia and a sacrum. NCM 143.949, WC 105-136. Six left scapulae.

Remarks. The tubers of the ilia are well-rounded and not triangular, nor are they laterally-protrusive. The pars descendens are narrow and unangled. The alae possess only a moderate ventrolateral ridge, and not a strong blade. Figures 3.12a and 6.35a show the ilium referred to '*B. calamita*' by Holman and Stuart (1991). The sacrum does not belong to *B. calamita* either. Its diapophyses are not widely flared, and its dorsal transverse crest is indistinguishable from modern



Glacial Channels near Bosley, Cheshire 1 Reservoir. 2. Boulder-clay. 3. River gravels. 4 Glacial sands and gravels. 5. Limit of boulder-clay. 6 Drumlinoid hill features. 7 Channels. 8 'Hump' channels. 9. River rock-cut gorge. 10. Esker and Kame ridges.



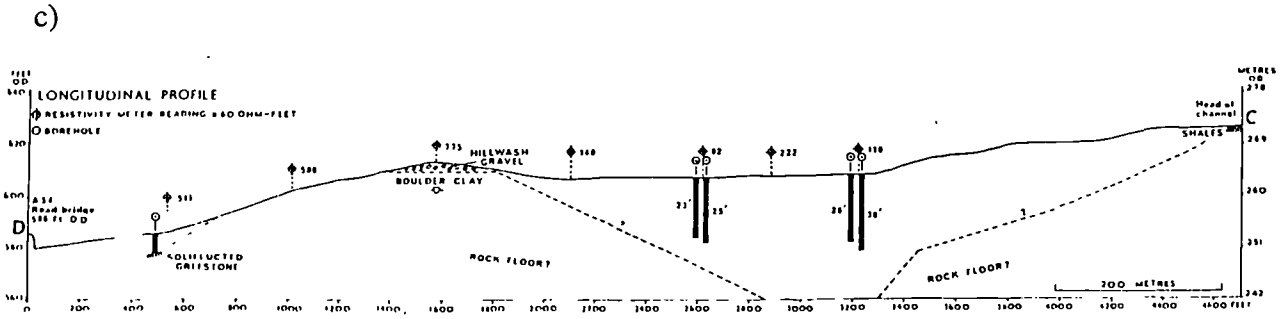


Figure 6.40: Whitemoor Channel, Cheshire: a) Location; b) Resistivity survey and interpretation of Lateglacial and Holocene deposits in transverse section through the Channel; c) Longitudinal profile of Channel deposits (after Johnson *et al*, 1970).

B. bufo. Also, the neural arch is not produced posteriorly, into two processes, as it is in *B. calamita*. The scapulae labelled were described as *Bufo* sp by Holman and Stuart (1991) but are also *B. bufo*. They lack the supraglenoid fossa of *B. calamita*.

6.6 Scotland

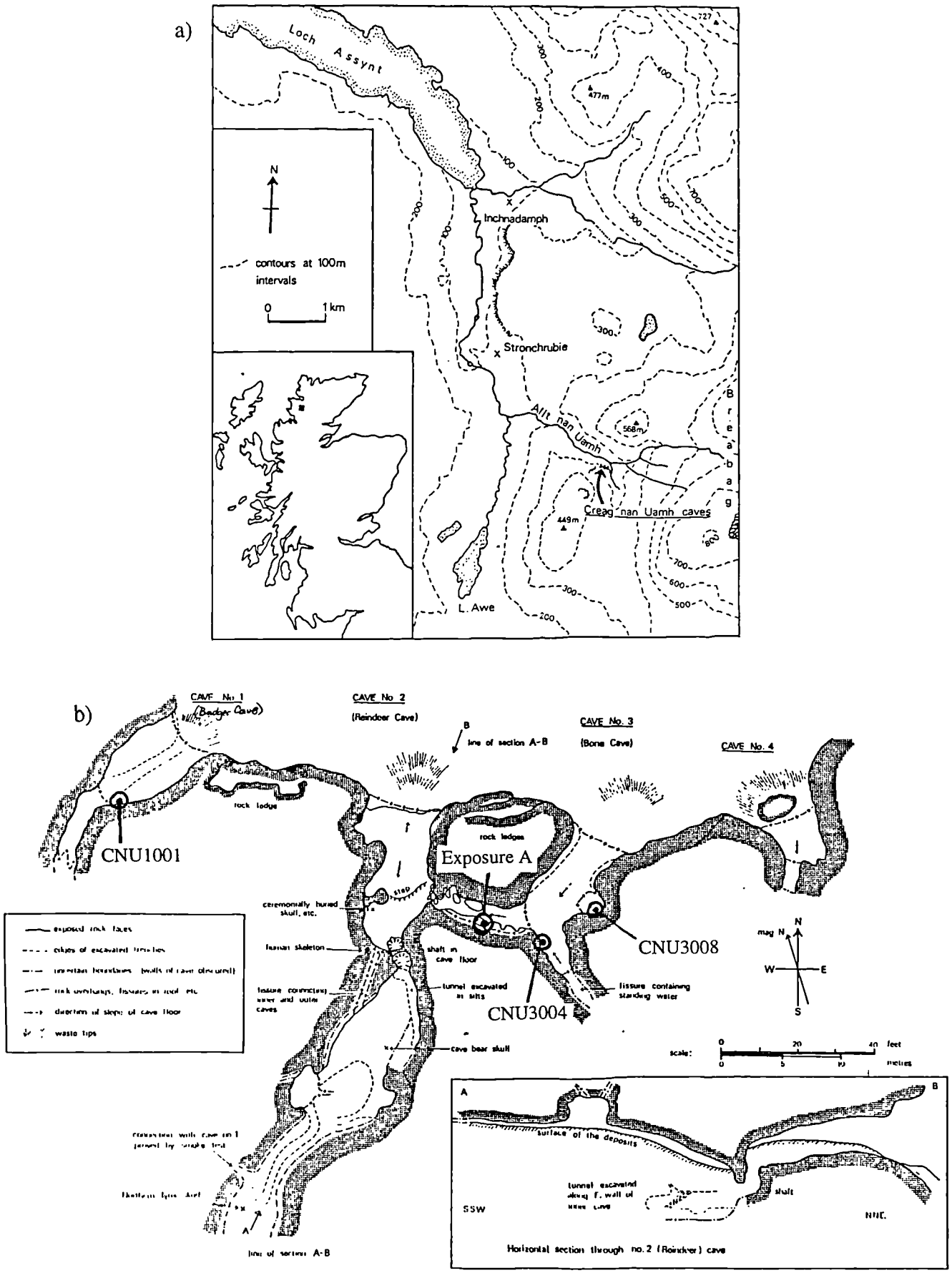
CREAG NAN UAMH CAVES, ASSYNT, SUTHERLAND, HIGHLAND REGION

The Creag nan Uamh caves (NGR NC276206) are situated beneath a crag on the north slope of Cnoc nan Uamh, overlooking the Allt nan Uamh valley, on the southwest face of the Durness Limestone plateau. Bone Cave was first investigated in 1889 (Peach and Horne, 1917), and all three caves were later excavated between 1926-7 by Callander, Cree and Ritchie. Only preliminary reports of their findings were published (Callander *et al*, 1927), but records of earlier excavations have been re-examined (Lawson, 1981). The stratigraphies from Bone Cave (Peach and Horne, 1917) and Reindeer Cave (Cree, unpublished, in Lawson, 1981) are shown in Figure 6.42. An account synthesising this data and indicating the present understanding of the caves' stratigraphy is given by Lawson (1995). Lawson has recently carried out small scale excavations of remaining pockets of cave earth in a passage which connects Bone Cave to Reindeer Cave (see Figure 6.41b). Further small scale excavations are anticipated on existing exposures and on the Foxes' Den rock shelter (Lawson, pers. comm., 1996).

A rich vertebrate fauna, including reindeer, brown bear, northern lynx, arctic fox, wolf and collared lemming, came mostly from the inner chamber of Reindeer Cave (Newton, 1917; Lawson, 1995). It has been suggested that reindeer antlers were deposited in Reindeer caves by humans, which would have made Creag nan Uamh the earliest human habitation site in northern Scotland (Lawson and Bonsall, 1986), but this idea is no longer tenable. Thirteen radiocarbon dates on mammal bone were obtained previously from Reindeer Cave. Apparent ages range from 44-28ka BP on the 'upper gravel' layer of the outer chamber and the 'pale yellow silty-sand' of the inner chamber (Lawson, 1995). None of the dates come from the overlying 'cave earth' of the outer chamber, which has been examined here. One date of 8,300±90 ^{14}C BP from the inner chamber is suggested to be indicative of burrowing activity by scavenging animals (Lawson, 1995), presumably contemporaneous with accumulation of Holocene deposits in the outer chamber. A programme of OSL dating is also being carried out by D. Sainty (Sheffield University) and a number of radiocarbon dates have recently been obtained by the National Museum of Scotland, although no results are available at present.

BADGER CAVE AND BONE CAVE

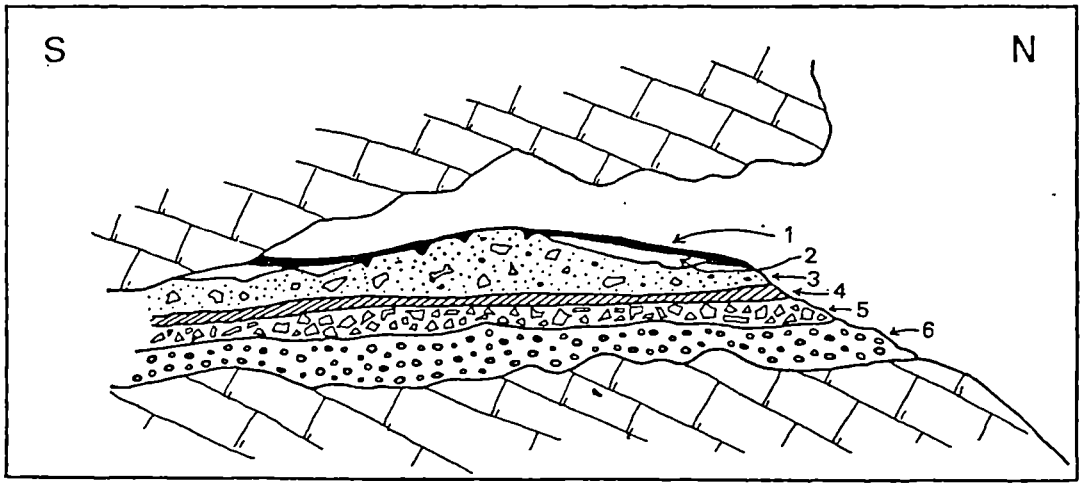
Figure 6.41 shows the relative locations of the caves. Reindeer Cave has not been studied as part of this project. A reddish brown cave earth, rich in vertebrate remains, was once present as an extensive layer in all the caves, though now only pockets remain (Lawson, 1995). This will be known here as the 'Red Cave Earth'. It was reported to contain a temperate fauna with human remains, red deer, roe deer, cow, sheep, pig, common frog, common toad, possibly natterjack toad, and a few reindeer antler pieces (Newton, 1917). In Bone Cave, the Red Cave Earth was capped by a 'whitish marl with pupa-like land snails' and a layer of sheep-dung (Peach and Horne,



(redrawn from the unpublished 1927 survey by McWilliams)

Figure 6.41: The Creag nan Uamh Caves, Highland Region: a) Location (after Lawson, 1981); b) Survey of the caves, showing sampling points (modified from Lawson, 1981).

a)

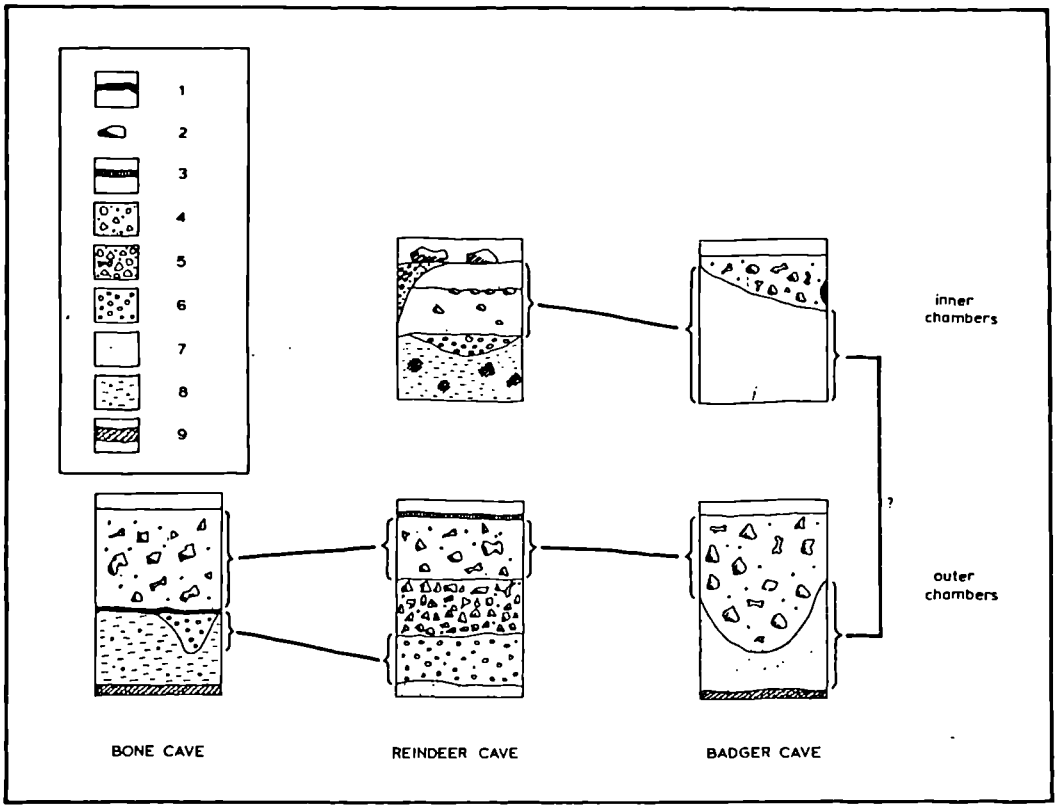


(redrawn from Peach & Horne 1917, 340)

Layer

1 Peaty layer – sheep dung.
2 Whitish marl – containing remains of shells of Pupa-like land snails.
3 Red cave earth – clay with limestone splinters. Many faunal remains, including species now extinct in Scotland. Presence of man indicated by 'hearths' (?). Wet and mild conditions.
4 Grey clay – derived from glacial debris from slopes of Breabag, shot into cave from surface of a valley glacier.
5 Limestone fragments – frost-shattered from walls and roof of cave's interior. Contained arctic fauna. Cave dry.
6 Gravel – well-rounded. Representing drainage through limestone from slopes of Breabag and limestone plateau. Water issued out of cave's mouth, as shown by imbrication of particles. Glaciers still in high ground to east?

b)



Suggested lithostratigraphy of the Creag nan Uamh caves. Key: 1. Speleothem deposit. 2. Breakdown material. 3. Sheep dung. 4. 'Cave earth'. 5. Faunal rich 'upper gravel' unit. 6. Water-lain gravel. 7. Silts and sands. 8. Clayey-silts. 9. Weathered dolomite.

Figure 6.42: a) Schematic lithostratigraphic section of Late Pleistocene and Holocene deposits in Bone Cave, Highland Region (after Lawson, 1981); b) Schematic representation of relationships between Late Pleistocene and Holocene deposits in the Creag nan Uamh Caves, Highland Region (after Lawson, 1995).

1917).

Recent small scale sampling by the author and T.J. Lawson, in Badger Cave and Bone Cave, has offered the opportunity for detailed analyses of the Red Cave Earth for herpetofaunal remains, which are discussed below. Sample numbers with the prefix 'CNU' were taken by the author from Badger Cave and Bone Cave in 1994. Sample CNU #1001 is from Badger Cave and samples #3001, #3004, #3008 are from Bone Cave. All samples are from the reddish brown Cave Earth. In Badger Cave this was present in pockets around the margins of the cave, from where samples were taken to be sieved and analysed. In Bone Cave, a small section called 'exposure A' was excavated at the south wall of the connecting passage with Reindeer Cave (T.J. Lawson, pers. comm., 1996). 'S. wall connecting passage, Feb '96' is a sample taken by Lawson from this section. Figure 6.41b shows the locations of the sampling points.

The concentration of bones in the sieved samples is extremely high, up to approximately 20% by volume. The great abundance of material and its excellent state of preservation suggests it is in primary context and probably accumulated over a reasonably long period of time. The animals represented may have hibernated and died in the cave, but their great numbers suggest that accumulation by raptors or carnivorous mammals is more likely. Pinto Llona and Andrews (1996, 1998) have identified that several mustelids, including badger and otter, are likely accumulators of amphibian bones in cave environments. Due to the great abundance of anuran bones, only their diagnostic elements and a representative selection of other elements have been removed. Should an exhaustive study be required in the future, without biased removal of particular elements, some bags of totally unsorted sieved residue have been retained. All newt, lizard and snake bones have been removed.

The small vertebrate material and sieved residues are presently in the author's possession, but will be housed in the Royal Museum of Scotland (Edinburgh) in due course. A full acount is only given for the sample from the south wall of the connecting passage between Bone Cave and Reindeer Cave, taken in February 1996. It produced the following taxa: *T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V. berus,* Ophidia indet. All four of the other samples examined produced exactly the same taxa (see Table 6.27), but time limitations of have prevented a full systematic description of the bones from these samples. It is estimated that in total, some 10,000 amphibian and reptile bones have been collected. Radiocarbon dates on herpetofaunal remains from Badger Cave and Bon Cave, and the genesis of the Red Cave Earth, are discussed in Chapter 7.

Table 6.27

CNU #1001 (Badger Cave)	*T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R.* *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis,* *V. berus,* Ophidia indet.

Exposure A (Bone Cave)	*T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V. berus,* Ophidia indet.
CNU #3001 (Bone Cave)	*T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V. berus,* Ophidia indet.
CNU #3004 (Bone Cave)	*T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V. berus,* Ophidia indet.
CNU #3008 (Bone Cave)	*T. helveticus, T. vulgaris/helveticus, B. bufo, Bufo* sp., *R. temporaria, Rana* sp., Anura indet., cf. *L. vivipara, A. fragilis, V. berus,* Ophidia indet.

Systematic palaeontology

Triturus helveticus

Material. 'S. Wall, connecting passage, Feb '96'. One cervical vertebra, four trunk vertebrae and one caudal vertebra. CNU #1001, #3001, #3004, #3008.

Triturus vulgaris/helveticus

Material. 'S. Wall, connecting passage, Feb '96'. One trunk vertebra, two femora, one humerus, one tibia, one ilium, two ribs, one right dentary, one atlas vertebra, three vertebrae and fragments.

Bufo bufo

Material. 'S. Wall, connecting passage, Feb '96'. Seven left and two right ilia, one left and one right scapula, four tibiofibulae, one right humeral fragment, four sacra, three male second digit metacarpals, one third vertebra, one left premaxilla, one right maxilla, one left frontoparietal and one fused right frontoparietal and prootic. A tibiofibula from this sample was submitted for AMS Radiocarbon dating (OxA-7293). CNU #1001, #3001, #3004 and #3008. Numerous ilia, frontoparietals, scapulae and other elements. A humerus from CNU #1001 was submitted for AMS radiocarbon dating (OxA-7294).

Bufo sp. indet.

Material. 'S. Wall, connecting passage, Feb '96'. Three left and one right ilia, two parasphenoids, three squamosals, one partial radioulna, one left dentary, one phalanx, two distal phalanges and several other elements. Numerous tibiofibulae, radioulnae, tibiales, fibulares,

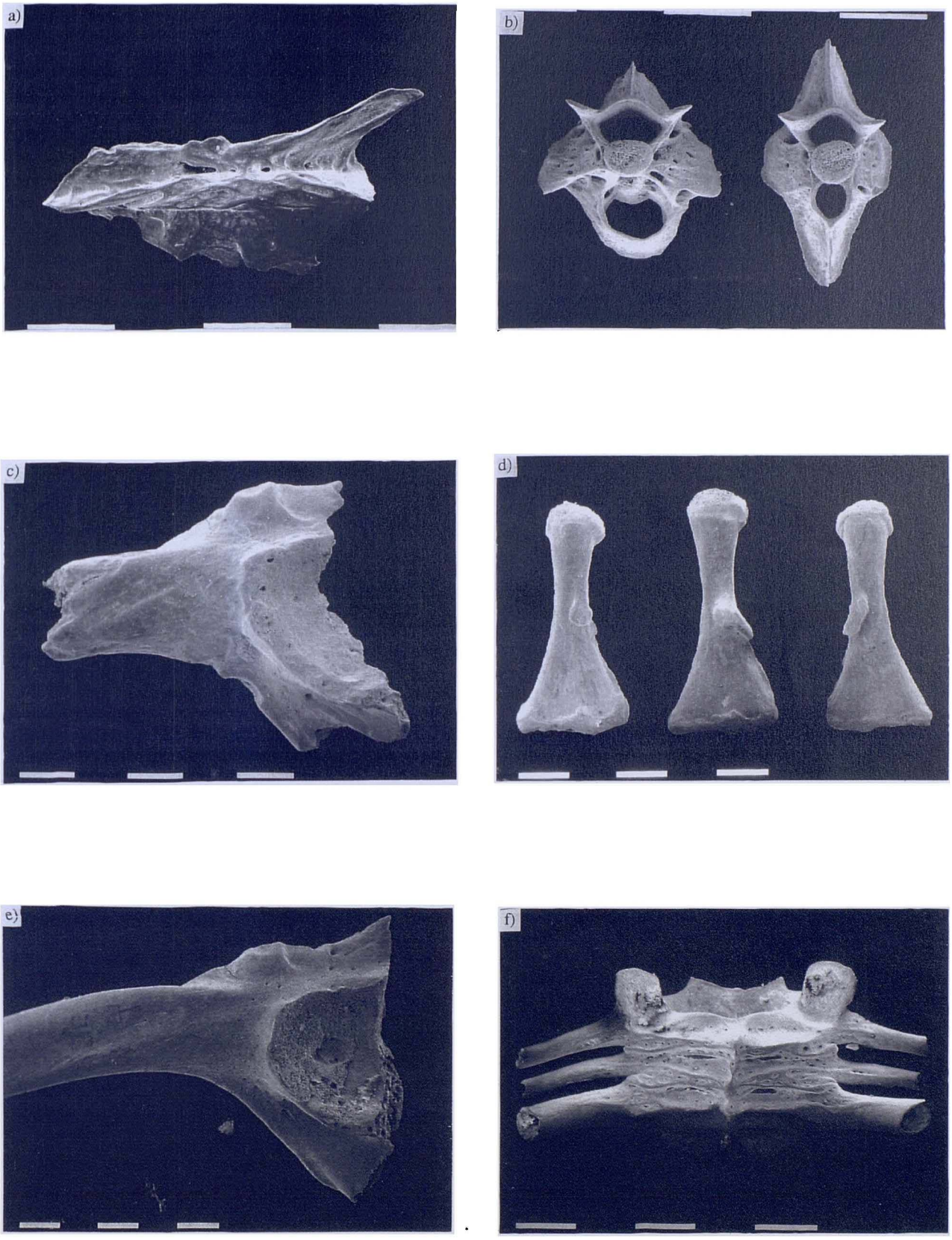
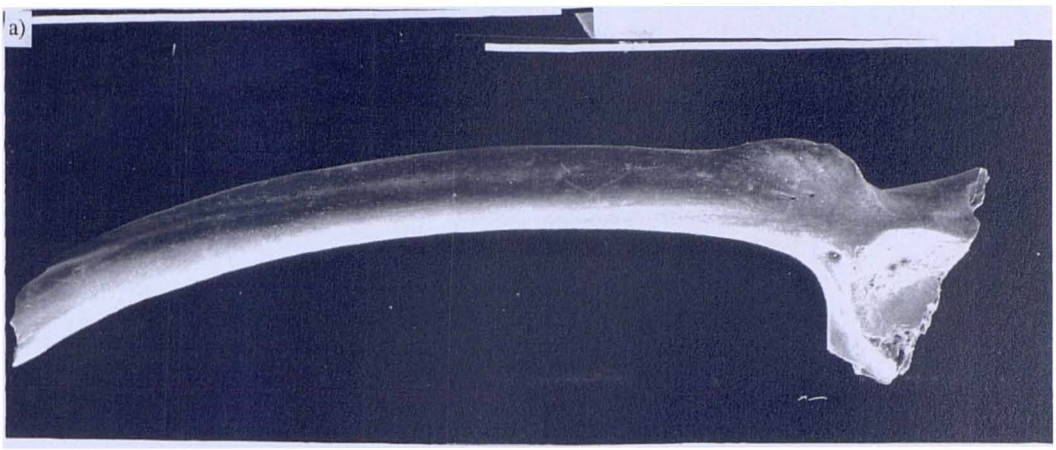
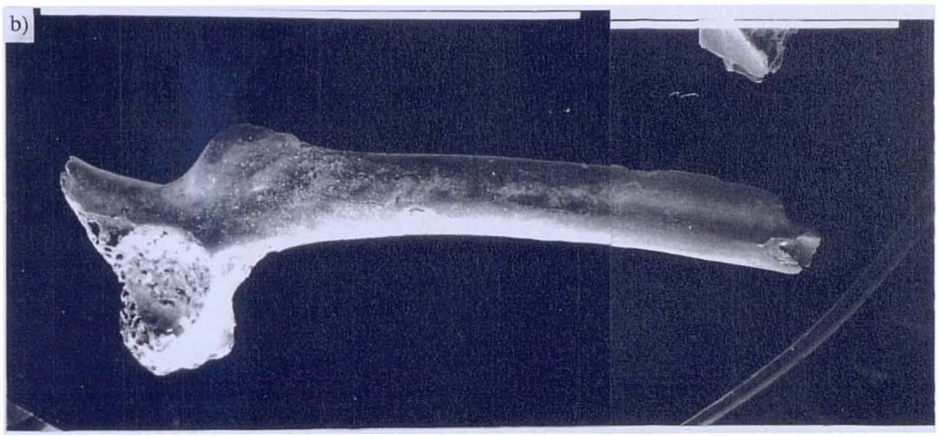
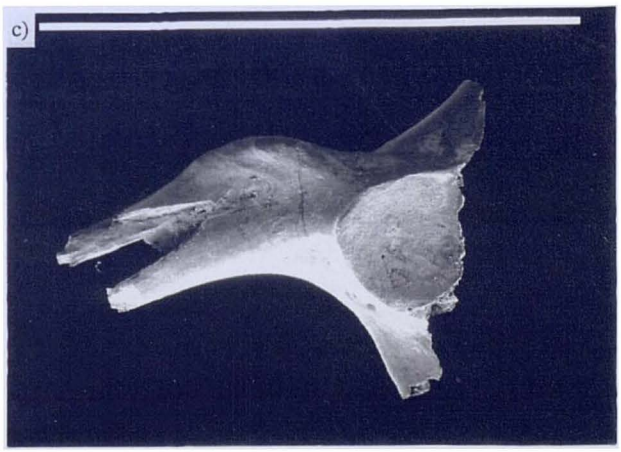


Figure 643: Amphibian remains from Badger Cave (b, e-f) and Bone Cave (a, c-d), Creag nan Uamh: a) right frontal (dorsal view) of *T. helveticus* (sample CNU 3001); b) cloacal (left) and caudal vertebrae (anterior view) of *T. helveticus* (sample CNU 1001); c) left ilium (lateral view) of *B. bufo* (sample 'S. wall, connecting passage', 1996); d) second digit metacarpals from mature males of *B. bufo* (sample CNU 3001); e) left ilium (lateral view) of *B. bufo* (sample CNU 1001); f) pathological fused seventh, eighth and sacral vertebrae (dorsal view) of *R. temporaria* (sample CNU 1001).







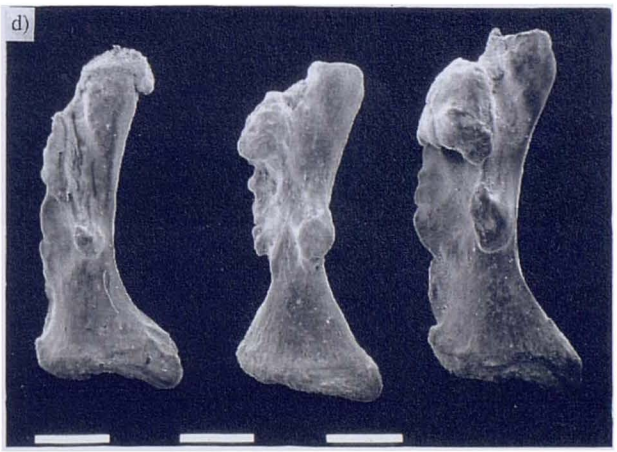


Figure 6.44:Remains of *R. temporaria* from Bone Cave, Creag nan Uamh (sample CNU 3001): a) left ilium, lateral view; b) right ilium, lateral view; c) left ilium, lateral view; d) right second digit metacarpals from mature males.

metapodials, phalanges, parasphenoids, squamosals, trunk vertebrae, sacra, maxillae, premaxillae, sphenethmoids and other cranial elements. CNU #1001, #3001, #3004 and #3008. Numerous tibiofibulae, radioulnae, scapulae, precoracoids, coracoids, quadratojugals, tibiales, fibulares, metapodials, phalanges, parasphenoids, hyoidal cornua, angulosplenials, dentaries, squamosals, trunk vertebrae, sacra, maxillae, premaxillae, sphenethmoids and other cranial elements.

Rana temporaria

Material. 'S. Wall, connecting passage, Feb '96'. Twenty left and thirteen right ilia, four left and three right scapulae, three left and three right humeri and two left frontoparietals. A humerus from this sample was submitted for AMS Radicoarbon dating (OxA-7291). CNU #1001, #3001, #3004 and #3008. Numerous ilia, humeri, frontoparietals and other elements. A left ilium from CNU #1001 was submitted for AMS radiocarbon dating (OxA- 7283), as was a humerus from CNU #3005 (OxA-7292).

Rana sp. indet.

Material. 'S. Wall, connecting passage, Feb '96'. Three tibiofibulae, one partial tibiofibula, three sacra, seven maxillae and fragments, five male second digit metacarpals, one atlas vertebra, one left dentary, one carpal, three metacarpals, three distal phalanges and several other elements. CNU #1001, #3001, #3004 and #3008. Numerous tibiofibulae, radioulnae, scapulae, coracoids, precoracoids, tibiales, fibulares, metapodials, phalanges, parasphenoids, squamosals, trunk vertebrae, sacra, maxillae, premaxillae, quadratojugals, sphenethmoids, angulosplenials, dentaries and other cranial elements.

Indeterminate Anura

Material. CNU #1001, #3001, #3004, #3008. Numerous urostyles, ischia, pterygoids, nasals, parasphenoids and other cranial elements.

cf. *Lacerta vivipara*

Material. 'S. Wall, connecting passage, Feb '96'. Three trunk and two caudal vertebrae, one right maxilla and one right ilium. CNU #1001, #3001, #3004 and #3008.

Anguis fragilis

Material. 'S. Wall, connecting passage, Feb '96'. Thirty-four osteoderms, one trunk vertebra, three partial caudal vertebrae, two ribs and one partial right dentary. CNU #1001, #3001, #3004 and #3008. Numerous osteoderms, trunk vertebrae, caudal vertebrae, ribs, dentaries and other elements. Four trunk vertebrae from CNU #1001 were submitted fo AMS radiocarbon dating (OxA-7296), as were four trunk vertebrae from CNU #3004 (OxA-7297).

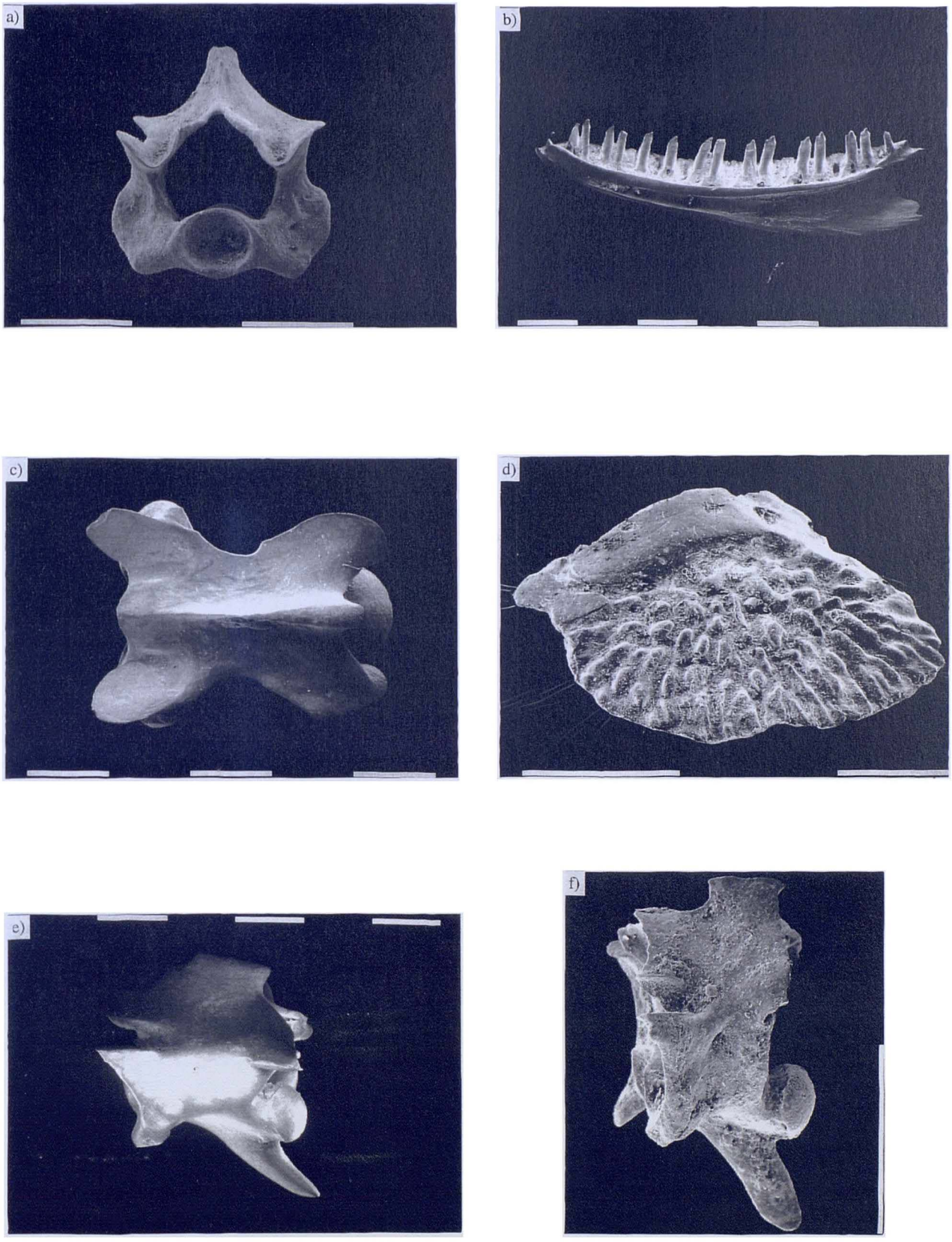


Figure 6.45:Reptile remains from Badger Cave (b, e-f) and Bone Cave (a, c-d), Creag nan Uamh: a) trunk vertebra (anterior view) of *L. vivipara* (sample 'S. wall, connecting passage'); b) right dentary (medial view) of *L. vivipara* (sample CNU 1001); c) trunk vertebra (dorsal view) of *A. fragilis* (sample CNU 3001); d) osteoderm (oblique external view) of *A. fragilis* (sample CNU 3008); e) trunk vertebra (left lateral view) of *V. berus* (sample CNU 1001); f) cervical vertebra (left lateral view) of juvenile *V. berus* (sample CNU 1001).

Vipera berus

Material. 'S. Wall, connecting passage, Feb '96'. Two partial trunk vertebrae and one caudal vertebra. CNU #1001, #3001, #3004 and #3008. Trunk vertebrae, caudal vertebrae and ribs. One trunk vertebra from CNU #3005 was submitted for AMS radiocarbon dating (OxA-7295).

Indeterminate Ophidia

Material. 'S. Wall, connecting passage, Feb '96'. One rib and one partial vertebra.

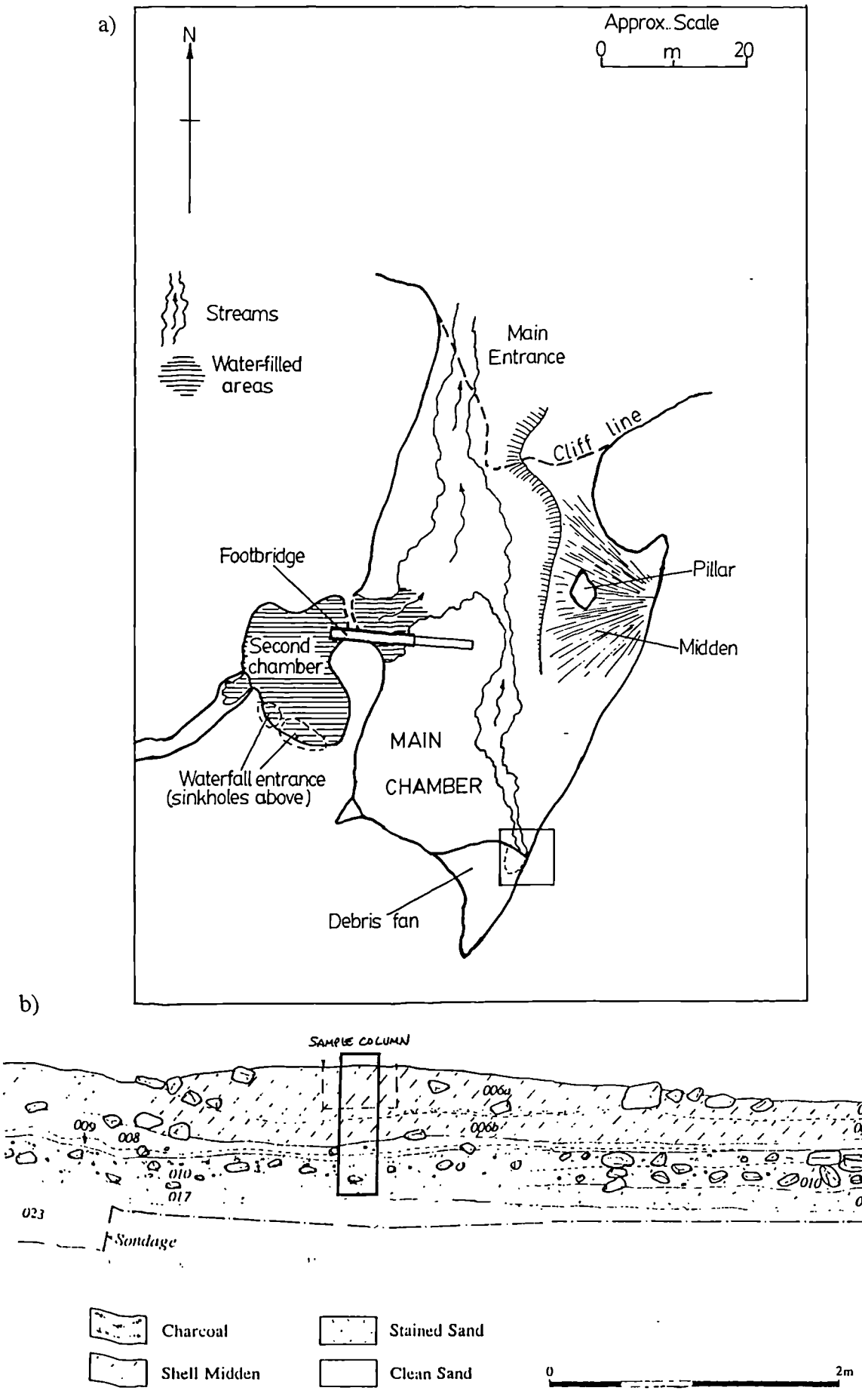


Figure 6.46: Smoo Cave, Highland Region: a) Plan of cave, showing location of midden and talus slope ('debris fan') (after Gleed-Owen, 1992); b) Section through midden, showing location of sample column (modified from Pollard, 1992).

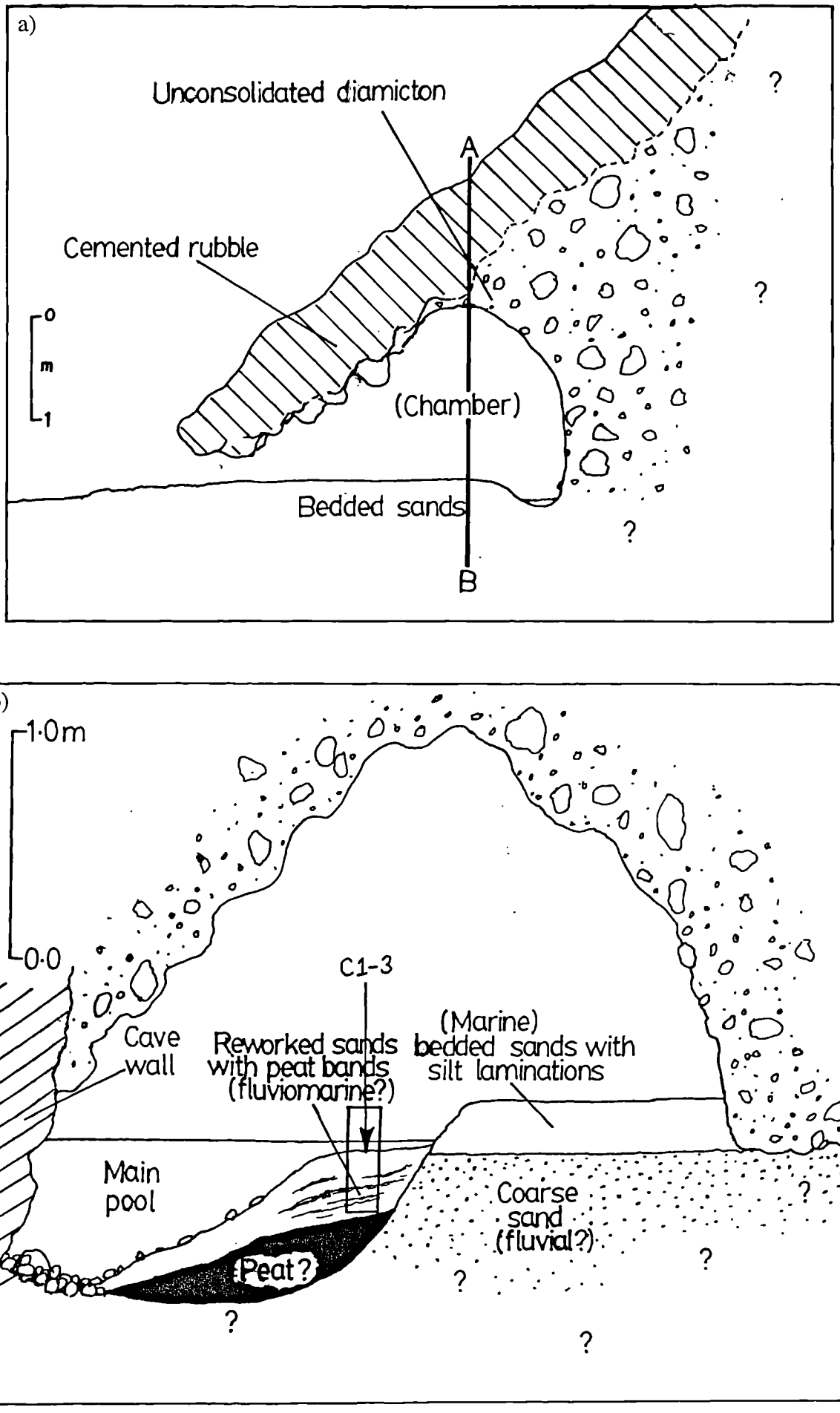


Figure 6.47: Smoo Cave, Highland Region: a) North-south section through ?Late Pleistocene talus slope and small chamber eroded beneath (after Gleed-Owen, 1992); b) East-west section through Late Pleistocene and Holocene deposits beneath talus slope, showing location of core C1-3 (modified from Gleed-Owen, 1992).

SMOO CAVE, DURNESS, SUTHERLAND

Smoo Cave (NGR NC419672) is situated near the village of Durness, on the north coast of Sutherland. It lies at the head of a 700m-long geo or gorge, along the lines of two parallel faults in Cambrian Durness Limestone, and probably developed during the Late Tertiary (Ford, 1959). The main chamber is a sea cave, but there are a network of other flooded chambers and choked phreatic passages. The main cavern contains a shell midden, which is currently eroded by high spring tides. It is thought to date to the Viking period around 1000-1500 BP but may involve earlier phases of inhabitance (T. Pollard, pers. comm., 1994). Small samples were taken in 1991, from the eroding midden face, for an undergraduate project (Gleed-Owen, 1992). The midden has since been excavated (1992) by the Glasgow University Archaeological Research Division, but the resulting vertebrate material has not yet been seen. A report by Pollard (1992) set out preliminary findings of this study, but a comprehensive description and interpretation of the midden is still lacking. Smoo Cave itself has been noted in various obscure literature (see references in Gleed-Owen, 1992), and was fairly comprehensively described and mapped by Pilling (1953). Despite this, no examination of unconsolidated sediments (except the midden) appears to have taken place, other than that carried out by Gleed-Owen (1992).

This is the northernmost site on the British mainland to produce herpetofaunal remains. Most of the material described below came from midden samples, taken by the author in 1991. Samples SM #1 to SM #5 were taken at 10cm intervals, in a vertical sequence from the eroding midden face (see Figure 6.46b). These contained abundant fish bones and fragments of large vertebrate remains, but relatively few amphibian or reptile bones. Those recovered were whitish in colour as might be expected from a late Holocene midden. Sample C #1-3 is from a short core (c.30cm depth) of silty sands interbedded with organic and silt laminations, obtained from a small chamber eroded beneath the cemented talus slope at the back of the cave (see Figure 6.47). The sediments are likely to have been deposited before the midden was in existence as the sequence appears to be continuous with the sediments which underly the midden (Gleed-Owen, 1992). They contained a high-energy intertidal assemblage of marine molluscs, ostracods and Foraminifera, particularly *Cibicides lobatulus* (c.97%). A bone of cf. *L. vivipara* from this sample is brown in colour, probably indicating an older age than for the bones in the midden. An amino acid racemisation determination on twenty foraminferal tests (*C. lobatulus*) from the core C1-3 gave a very low ratio of 0.021 (G. Sykes, pers. comm., 1992) and suggests that the sediments are Holocene in age. Some of the sands and silts beneath the talus slope are very compressed, perhaps implying that they are older than the talus slope itself.

The bones from each sample are individually numbered in the account below. They are currently in the author's possession but will be housed in a museum in due course. The total herpetofaunal list is as follows: *B. bufo, Bufo* sp., *R.* cf. *temporaria,* cf. *R. temporaria*, cf. *L. vivipara*. The taxa recovered from each sample are shown in Table 6.28.

Table 6.28.

SM #1	*Bufo* sp., cf. *L. vivipara*
SM #2	*B. bufo, Bufo* sp., *R.* cf. *temporaria*, cf. *L. vivipara*
SM #3	*B. bufo, Bufo* sp., cf. *L. vivipara*
SM #4	*Bufo* sp., cf. *R. temporaria*, cf. *L. vivipara*
SM #5	(No herpetofaunal remains)
SM #6	cf. *L. vivipara*
C #1-3	cf. *L. vivipara*

Systematic palaeontology

Bufo bufo

Material. SM #2/2. One right scapula. SM #2/3. One trunk vertebra. SM #3/3. One left coracoid.

Remarks. The scapula lacks any form of fossa supraglenoideum. The coracoid is identical to recent *B. bufo* and not as widely flared distally as *B. calamita.*

Bufo sp. indet.

Material. SM #1/1. One right radioulna. SM #2/1. One tibiale. SM #4/3. One fibulare. SM #4/1. One right humerus. SM #3/4. Two tibiales and one fibulare. SM #3/5. One metatarsal and two phalanges.

Remarks. The radioulna is straight and relatively slender, with a deep foramen on its medial proximal side. The other elements compare well to modern *B. bufo*, and at such a northerly location, it is very unlikely that any of them could belong to any other bufonid.

Rana cf. *temporaria*

Material. SM #2/4. One left angulosplenial.

Remarks. The angulosplenial has only a shallow external sulcus, which continues beyond the posterior edge of the coronoid process, and thus belongs to *Rana*. The bone is also straighter and more slender than *Bufo*. Its coronoid process is high and more angular, and produced into a posterior fin-like crest. It matches recent specimens of *R. temporaria* closely, and is unlikely to belong to another species, but the possibility of *R. arvalis* being present in northern Scotland must be considered.

cf. *Rana temporaria*

Material. SM #4/2. One male left humerus.

Remarks. This humerus lacks its distal articulation, but has medial and lateral cristata. These are moderately developed and not widely flared as in *Bufo* or green frogs. However, they are not posteriorly directed as would be expected in *R. temporaria*, though this may be due to immaturity of the animal. The cristata end dorsally, only half way up the shaft, and though this appears to belong to *R. temporaria*, there is some doubt.

cf. *Lacerta vivipara*

Material. SM #1/3. One right humerus. SM #2/6. One left femur. SM #6/2. One posterior half of a caudal vertebra. C #1-3. One cloacal vertebra. SM #3/1. One left innominate bone. SM #3/2. Left femur. SM #4/5. One presacrum and one sacrum.

Remarks. Though small lacertids are difficult to identify, it is unlikely that any other species could have reached this far north during the Holocene. These bones are small and indistinguishable from modern *L. vivipara*. They are unlike *L. agilis* in size and morphology. The humerus is incomplete, with its proximal end missing. The epiphyses of the femur are damaged, but it is otherwise identical to a the femur of a modern *L. vivipara* specimen with a snout-vent length of 46mm (CGO 41/1). The half caudal vertebra is identical to those of the modern specimen, in size and shape. Though the vertebra may have been autotomised, it was probably detached from its anterior half after death. The presacral vertebra can be recognised by its relatively short length (approximately equal to its width), and its slender transverse processes, unlike the more robust sacral vertebrae. It is the only brown bone found, and came from sediments pre-dating the midden. The innominate bone is named as such here as it consists of an intact ilium, ischium, and partially intact pubis. It is slightly more robust than that of CGO 41/1, but with the same overall dimensions. The tuber superior is posteriorly angled, and more robust than the recent specimen. The left femur has its epiphyses missing, but is also of almost identical proportions, though perhaps slightly more robust in diaphyseal section. The presacrum is smaller than the sacrum, and these are not from the same individual. The sacrum is approximately the same size as that from CGO 41/1 (46mm snout-vent), but its transverse processes are much more robust: at least twice as broad anteriorly.

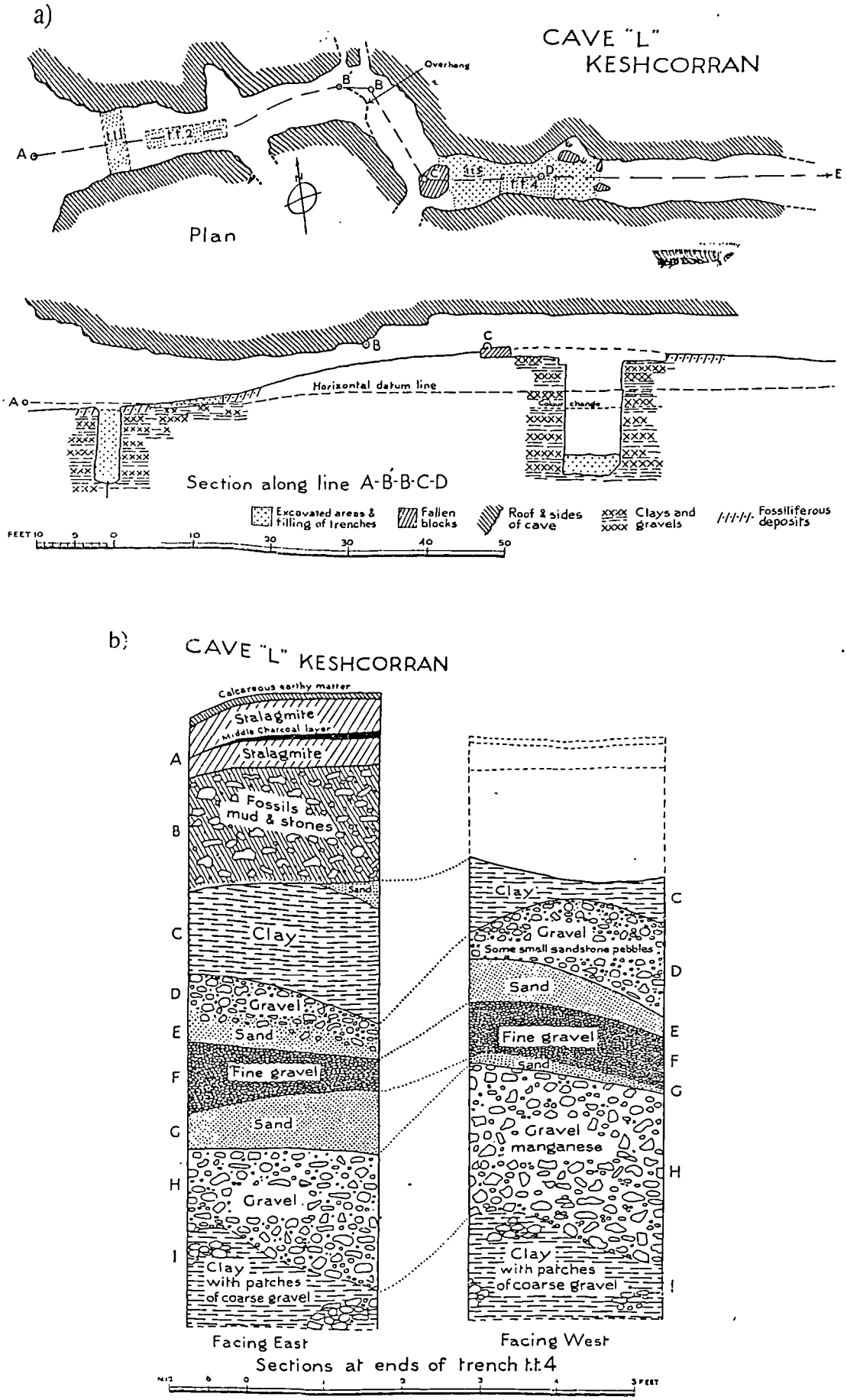


Figure 6.18: Coffey Cave (aka Cave 'L'), Co. Sligo: a) Plan of cave, showing areas excavated by Gwynn *et al* in 1929 ; b) Schematic lithostratigraphic section through Late Pleistocene and Holocene deposits (after Gwynn *et al*, 1940). Coffey Cave is adjacent to Plunkett Cave and this is the only section drawing available.

6.7 Ireland

PLUNKETT CAVE, KEISHCORRAN, CO. SLIGO, IRELAND

These are a series of about eleven inter-connected caves in a southwest-facing Carboniferous limestone crag on Keishcorran Mountain in central County Sligo, c.18km south of the town of Sligo (NGR G70101020). Early investigations in 1901 were led by R.F. Scharff who carried out excavations in two caves, Coffey Cave and Plunkett Cave, named after members of his team (Scharff *et al*, 1902). Gwynn *et al* (1940) later named the caves using letters (Coffey Cave = 'J') and detailed new work carried out in cave 'L' in 1929. The spelling Keshcorran was used in this early literature. Coffey cave was described as one of the larger caves, with an A-shaped mouth and lying about central in the series (Scharff *et al*, 1902). A trench was cut across the mouth of the cave and its stratigraphy was detailed as a blackish brown surface soil 15-30cm thick, which contained a red deer antler tine, domestic animal remains and implements described as like those 'commonly found in raths and crannogs'. Beneath this layer was a breccia consisting of a calcareous tufa with fallen limestone blocks and fragments, 30cm thick in the middle but reached about 1m towards the sides of the cave. It contained numerous land-snails (*Helix, "Hyalinia", Clausilia*) and small mammal bones including arctic lemming, stoat and an unidentified canine. Beneath the breccia, a brown ochreous clay containing large limestone blocks was excavated to a thickness of 2m before digging was abandoned. The clay yielded arctic lemming and numerous other undetermined small mammal bones. No section drawings or faunal lists were given. Gwynn *et al* (1940) continued work in Coffey Cave which they named Cave 'L'. A plan and section drawing from a trench dug 15m along the almost linear passage is shown in Figure 6.48. No drawings are published for Plunkett Cave described below. Faunal additions recorded by Gwynn *et al* from the 'brown earth' were grouse, probably a thrush and blackbird (*Turdus* spp.), undetermined small birds and possibly Irish elk. The authors noted their concern that recent domestic animals and frog remains appeared to be intrusive. They considered the brown bear, fox, reindeer, hare, lemming and field mouse to be an integral fauna deposited under tundra conditions, thus suggesting that the brown earth is largely of Devensian age.

Plunkett Cave is a smaller cave located towards the southern end of the series, with its entrance diminishing to a low mouth less than 2m high (Scharff *et al*, 1902). It extends for over 15m where a gallery branches off to the right for 6m. This gallery then opens into the Sloping Chamber and itself branches off to the left into the Water Gallery, parallel to the entrance passage. The 'surface stratum' varied from 15-60cm in thickness and contained varying amounts of calcareous tufa which was almost pure in places (Scharff *et al*, 1902). Layers of charcoal were noted as well as Neolithic and Bronze Age implements and marine molluscs. A few human remains were found in the 'Sloping Chamber', along with very numerous bones and teeth of horse, ox, sheep, goat, pig, dog, fox, rabbit and less abundant remains of red deer, hare, badger and a single bone of reindeer. This is clearly a mixed assemblage as it includes Devensian (reindeer) and late

Holocene (rabbit) elements. The activities of rabbits may have been responsible for this. Towards the bottom of the layer, occasional bones of brown bear were found in places. Numerous bones of field mouse and frog were also recorded. Beneath this layer was a brown or ochreous fairly sandy clay which extended throughout the cave. Within it, large boulders were noted including some which were apparently striated. The vertebrate fauna included brown bear, fox, wolf and red deer. Three rabbit bones were probably introduced by burrowing. Again, frog and field mouse was encountered repeatedly. Lemming was found once near the cave entrance, but no other small mammals were recorded. Deep sections were dug in several parts of the cave, wherein the clay became yellow and barren of remains with depth (Scharff *et al*, 1902).

It is most probable that this was the cave investigated by the current author on a visit in December 1995. The surface sediments were mainly a dark mixture of guano and sheep droppings, but a sample of the underlying cave earth was taken to a depth of about 20-30cm from inside the main entrance passage. This is probably the 'surface stratum' described by Scharff *et al* (1902). Its age is presumably Holocene due to its stratigraphic position at the surface, but as Scharff *et al* recorded arctic lemming from this layer, a Lateglacial age is possible. Scattered recent rabbit remains and evidence of burrowing suggests that the cave's sediments are actively disturbed by rabbits. As most of the cave's sediment fill remains intact, there is clearly potential for further excavation at the site.

One sample of around 2kg was taken and sieved for herpetofaunal remains. The material is currently in the possession of the author.

Systematic palaeontology

Rana temporaria

Material. Three left and four right ilia, two left and two right frontoparietals, three male left humeri (one pathogenic).

Remarks. The ilia are in excellent condition and generally complete. They typically have a relatively low vexillum with ribbed tubers. The vexillums are depressed at a fairly consistent height along their length. The pathogenic humerus has undoubtedly resulted from a bad dislocation of the lower forearm. The radioulna must have been repositioned outwards (laterally) during life, and eroded the lower ball joint of the humerus, creating a second trochlea. The original trochlea displays extra pathogenic growth, probably required to facilitate the extra muscle growth required to keep the joint functional.

Rana sp. indet.

Material. Six partial or complete femora, seven partial or complete tibiofibulae, three radioulnae, three coracoids, one fused tibiale and fibulare, three tibiales, three fibulares, five metacarpals, one carpal, three male II metacarpals, one atlas vertebra, three sacra, one left and one right angulosplenial, four parasphenoids, one left and one right maxilla, one clavicle, one left

squamosal and one right pterygoid.

Remarks. Some of the scapulae have a particularly strong dorsomedial ridge, developed into a strong process stretching from the the edge of the glenoid cavity to the distal blade. This is typically strongest around its mid-point, where its concave sides rise to a narrow ridge, giving the scapula as much depth as width at this point. It is effectively analogous to the acromion of the mammal scapula, but is positioned on the dorsomedial rather than the ventrolateral side.

Indeterminate Anura

Material. Thirteen trunk vertebrae, two humeri, three radioulnae and three limb bones.

Remarks. The vertebrae show a very large amount of variation, which throws some doubt on the diagnosis of anuran vertebrae. These are all likely to belong to *R. temporaria,* but cannot be identified as such by using constant characters. Therefore, strictly speaking, they must be referred as indeterminate Anura. One vertebra is very narrow, with a well-rounded neural spine, and with no obvious transverse ridge. Another has a very strong transverse ridge, somewhat posteriorly-deflected, and rising with a very strong neural spine to produce a rough tubular spine. This is steeper than in green frogs, but is evidence of variability on a scale which may cause problems when attempting specific diagnosis from vertebrae.

DERMOT AND GRANIA'S BED CAVE, BRICKLIEVE MOUNTAINS, CO. SLIGO

This cave is in a Carboniferous limestone crag on the eastern edge of the Bricklieve Mountains in County Sligo, c.18km south-southeast of the town of Sligo (NGR G70451035). Its entrance overlooks Lough Arrow, and is located just below High Wood and the Red Earl's Road. Its entrance is about 2.5m high and 5m wide, and is clearly formed along horizontal bedding planes. The cave extends for around 10m, but the ceiling then becomes too low to enter. A recess in the south wall extends for several metres. The cave is still used for keeping sheep and the floor has a covering of sheep droppings. No previous work has apparently been carried out in the cave.

During a visit in December 1995, a 2kg sample of wet peaty mud was taken from the cave floor. This did not appear to be of any great age but contained a few obvious frog long-bones. The fine limestone gravel residue (c.200g) contains particularly abundant coleopteran remains as well as frog, bird and mammal bones. There are also numerous well-preserved seeds and plant remains. All amphibian bones have been removed. Most of the frog bones show some signs of digestion and many are badly corroded, cf. those digested by badgers in Pinto Llona and Andrews (1998). Most are brown in colour, probably due to digestion, but a few are whitish. Virtually all of the bones are from adults and many are evidently from very mature animals.

Systematic palaeontology

Triturus vulgaris

Material. One trunk vertebra.

Remarks. The vertebra has a low, flat-topped posterior neural arch with a deep W-shaped posterior notch and wide ventral laminae.

Rana temporaria

Material. Four left and two right ilia, one male right humerus.

Rana sp. indet.

Material. Nine tibiofibulae, ten partial tibiofibulae, six femora, one partial femur, one male right humerus, two right humeri, one partial male left humerus, one partial right humerus, one juvenile left humerus, three radioulnae, one partial left and one right ilium, three ilial alae, four right premaxillae, four right maxillae, one atlas vertebra, nine trunk vertebra, two sacra, two partial vertebrae, two left and four right scapulae, one partial right scapula, three tibiales, four fibulares, one left and two right angulosplenials, four coracoids, fourteen metatarsals and pedal phalanges, three female metacarpal II, one sternum, two omosternums, one partial left frontoparietal, one distal manual phalanx, three distal pedal phalanges, one right suprascapula.

Indeterminate Anura

Material. One partial ilium, one partial right ilium, twelve vertebral fragments, one partial

atlas vertebra, two precoracoids, one juvenile precoracoid, three radioulnae, one partial radioulna, one partial juvenile radioulna, two femoral fragments, one urostyle, two partial urostyles, three ischia, one partial ischium, two parasphenoids, one partial parasphenoid, one right humerus, one partial right humerus, one humeral fragment, two nasals, three prootics, two left exoccipitals, one right suprascapula, one partial suprascapula, one hyoidal cornu, one sphenethmoid, three right pterygoids, one left and one right partial squamosal, forty-four metapodials, phalanges and partial long bones.

PIG CAVE, BRICKLIEVE MOUNTAINS, CO. SLIGO

This small cave (NGR G70401040) is not marked on maps but was 'discovered' during a visit by the author in December 1995. It is located at the north end of the Bricklieve Mountains in County Sligo, c.18km south-southeast of Sligo Town. It has been named Pig Cave because a pig mandible was found by the author whilst sampling loose cave earth. It is situated at the head of a short, steep-sided valley with no obvious water course, that was probably formed by cavern collapse. The geology is Carboniferous limestone. The cave enters the west side of the valley, and is accessible for about 15m before it is choked by boulders and roof collapse.

The back of the cave was choked with fallen blocks, and crevices between these were covered in a loose brown cave earth. This consisted of a silty sand and gravel and contained obvious large vertebrate remains including the left mandible of a pig, and fairly abundant small vertebrate remains including frog long-bones. Its age is not known, but it is probably Holocene. No stratification was noted within the sediment and it was sampled in bulk.

A sample of c.2kg was taken from the cave earth, and the resulting c.500g of sieved residue was examined for herpetofaunal remains, though not exhaustively. Frog bones are very numerous within it, and abundant coleopteran remains, some seeds and one land snail (*Oxychilus cellarius*) were noted. The frog bones are mainly stained dark brown, but some are a lighter tan or creamy colour. There is a fairly high occurrence of pathogenic deformity in the bones. Most of the frog bones are from mature adults, and probably males. Many bones clearly show signs of crushing, breakage and heavy digestion by predators. A detailed taphonomic study would be worthwhile. This assemblage is likely to be of predatory origin rather than a life assemblage.

Systematic palaeontology

Triturus vulgaris

Material. One trunk vertebra.

Remarks. The vertebra has a low, flat-topped posterior neural arch. Its zygapophyses are unusually produced, almost cf. *T. marmoratus*, and unlike recent specimens seen from southeast England.

Triturus sp. indet. (*vulgaris* group)

Material. One trunk vertebra (immature) and one caudal vertebra.

Remarks. These are slightly damaged and not distinct enough to allow specific diagnosis.

Rana temporaria

Material. Three left and ten right ilia, two male left humeri and one pathological male right humerus.

Remarks. Several of the ilia are complete, the rest have been crushed, broken and digested like many of the other elements.

Rana sp. indet.

Material. One trunk vertebra, five left and one right frontoparietals, one partial fused atlas and second vertebra, three male metacarpal II's, thirteen tibiofibulae and fragments thereof, six femora and fragments thereof, one female left humerus, three left and three right humerus, two male right humeri, two atlas vertebrae, seventeen trunk vertebrae, three sacra, two left and four right scapulae, two left and three right angulosplenials, two left and two partial right maxillae, two left squamosals, one right dentary, two sphenethmoids, four left and one right premaxillae, two coracoids, one sternum, two omosternums, three tibiales, one fibulare, two metatarsals,

Remarks. One of the trunk vertebrae has a bifurcated right transverse process, with the branches connected by a thin lamina. One of the male right humeri has its cristae cf. *Bufo*, though the posterior surface of the trochlea is much more vertically extensive and the medial epicondyle is not as wide. This may be a pathogenic state, but both cristata have strongly curved outlines and coalesce medially near the base of the posterior side of the shaft. The large size of many elements and the preservation of epiphyses on several bones indicates a prevalence of mature animals.

Indeterminate Anura

Material. Eight urostyles, one parasphenoid, two right pterygoids, one right nasal, one right exoccipital, two prootics, one vomer, six radioulnae, three precoracoids, three ischia, three coracoids, twenty metapodials and phalanges, one partial left humerus, five vertebral fragments, one partial tibiofibula and three long bone fragments.

Remarks. One urostyle has a pathogenic thickening associated with a fracture.

7 Taphonomic, dating, ecological and geographical issues - a discussion

7.1 Taphonomy of fossil herpetofaunal assemblages

Stuart (1982) observed that cave and fissure deposits tend to contain much more vertebrate material than other depositional environments such as fluvial sediments. A cave acts as a particularly effective repository for small vertebrate remains, and tends to preserve them well. This has been proven in practice for herpetofaunal remains, both by previous authors (e.g. Newton, 1917; Jenkinson, 1984; Holman, 1985, 1988) and in the experience of the current author. Of the sites studied during the current project, by far the richest faunal remains (in terms of abundance) have come from cave sites. This is no doubt a combination of taphonomic factors, ranging from the effective initial concentration of remains by predators (Stuart, 1982; Andrews, 1990; Pinto Llona and Andrews, 1996, 1998) to the spatially-constrained, relatively sheltered and low-energy conditions of the cave environment. Occasionally, rich bone accumulations occur in fluvial, lacustrine and other unsheltered environments. Nevertheless, these environments are usually less protective towards accumulations of vertebrate remains, with degradation and dispersal normally being much greater.

For herpetofaunal remains, some selective preservation appears to occur especially with a bias towards more robust elements, but there is no evidence from the work reported here to suggest that smaller species are under-represented due to taphonomic processes. It is notable that the most delicate of skeletal elements such as the caudal vertebrae of *T. vulgaris* are often present alongside the much larger and stronger elements of bigger species. Since all amphibian and reptile skeletons have roughly similar numbers of skeletal elements (well within one order of magnitude) initial concentrations of bones would be similar for individuals of any species. The commoner species ought theoretically to enter greater numbers of bones to the record, but the complexities of taphonomic processes make it difficult to base much inference on the relative abundances of species. Selective predation must also play an important role, either due to preference or availability and ease of capture. In a Quaternary fossil context, the presence of a species itself rather than its abundance, is arguably of greater value in palaeoenvironmental and biostratigraphic terms. However, the taphonomic study of herpetofaunal remains (e.g. Pinto Llona and Andrews, 1996, 1998) should in the future produce valuable additional information on predator-prey relationships and post-mortem processes.

For a particular sedimentary environment, there is bound to be a strong bias in the fossil record towards the fauna which was present locally. Despite the tendency towards more numerous preservation of bones in caves than in unprotected environments, local zoogeographic and ecological factors may be important in determining the actual species record that survives as a fossil assemblage. Indeed, the largest herpetofaunal assemblage (fourteen species) from the British Isles

to date was not from a cave but from a fluvial/estuarine deposit (Holman *et al*, 1990). This may be related to the fact that caves are often located in elevated areas where suitable water bodies for amphibian breeding or reptile foraging are lacking, or where vegetation is not conducive to a diverse range of herpetofaunal species. In fact, the general topography, drainage and vegetation in the vicinity of limestone caves tends to contrast quite strongly with that of wetland and riparian environments. The herpetofaunal species present in an area are thus likely to reflect such differences. Notwithstanding this, there appears to be no evidence to suggest that species present fairly locally are not included in fossil faunal assemblages from caves. Predators seem to be very adept at taking a wide cross-section of local fauna and depositing their remains within caves. However, strictly speaking, there is no knowing when an absence really is an absence and not a lack of representation. This problem should largely be overcome by the recognition of consistent faunistic patterns paralleled at different sites.

TAPHONOMY OF THE TORBRYAN CAVES HERPETOFAUNAL ASSEMBLAGES

The condition of the bones varied greatly, with most of the longer anuran bones being broken. Fragile cranial elements were less in evidence than the more robust vertebral and appendicular bones. As is generally the case in cave environments, anuran remains were found in greater numbers and volume than the other species. Anuran ilia are most frequently used in their identification sub-fossil, however the material studied here was often fragmentary and other elements, in particular the scapulae, sacrum and tibiofibulae, were useful. For the non-anuran species, vertebrae were the most commonly retrieved and identifiable elements. There appeared to be no obvious taphonomic bias against smaller species or delicate skeletal elements. Even the smallest and most fragile bones, such as newt caudal vertebrae, were well-preserved. Their relative paucity, therefore, is probably a true reflection of their initial concentration. Non-anuran remains are typically biased towards the more numerous (and robust) trunk vertebrae, with few cranial elements surviving.

Considering the valley-side nature of the deposits at Broken Cavern, and given that *A. fragilis* leads a mainly fossorial existence, it has been questioned whether fossil remains of this species could be found 'out of context', i.e. that younger remains could be incorporated into older deposits through burrowing (A.P. Currant, pers. comm.; A. Roberts, pers. comm.). However, this demands that not only did *A. fragilis* burrow into older deposits, but it died there also. It is surely more parsimonious to suggest that its remains arrived there through contemporary incorporation by raptors and small carnivores, as did the associated fauna. In support of this, an AMS date on *A. fragilis* from middle Holocene (Neolithic) Context 25 gave a suitably middle Holocene age, very similar to other dates on fauna from the same context (see below and Chapter 8).

NOTES ON THE TAPHONOMY OF WOOKEY HOLE HYAENA DEN

The herpetofaunal material is mostly very fragmented and consists of bones which have come from more than one source. Most of the remains are not identifiable to species or even genus (see systematic palaeontology section) and there is very clear evidence for *post-mortem* transport. Some of the remains are in very good condition, with little breakage or wear, even though some are very fragile. Conversely, much of the material is fragmentary, either broken but still with sharp edges or rolled so that all corners are well-rounded. Breakage in some cases probably occurred *in-situ* by trampling, but in others it must have occurred prior to this during fluvial transport to the depositional site.

The range of preservation conditions represented here are comparable to some of those discussed by Pinto Llona and Andrews (1996; 1998) and to those found at many other sites by the current author. The remains from the Hyeana Den are, however, unusual in displaying a broader range of conditions than seen elsewhere, within one assemblage. At least some of the material appears to have entered the cave without much damage, but much of it has been rolled. This accords with the water-lain nature of the sediments (R. Jacobi, pers. comm., 1997). None of the material would have survived digestion by hyaenas, and it is not known if raptors or smaller predators were involved in bone accumulation. Several mustelid species prey on amphibians, including otters and polecats, and their scats contain identifiable skeletal elements (Andrews and Pinto Llona, 1998).

7.2 Dispersal and immigration - some ideas and concepts

Very little work has been carried out on dispersal rates of amphibians and reptiles in modern environments. Menzies (1962) monitored the spread of *R. ridibunda* after its release on the edge of Romney Marsh in 1934-5. Over the subsequent years, the frogs dispersed at a rate of approximately 1 km per year. *R. ridibunda* is a very aquatic species, and therefore spends little time traversing terrestrial areas (Arnold and Burton, 1978; Necas *et al*, 1997). Thus, it is possible that more terrestrial species such as *R. temporaria*, *R. dalmatina* and *B. bufo* might be able to cover greater distances. Green frogs mature faster than brown frogs though (Smith, 1969), which may mean that a greater dispersal rate is possible. The suitability of adjacent habitats, and the availability of breeding places, must also be important controls. Theoretically, the environmental situation at the beginning of an interglacial cannot be reconstructed entirely, but the introduction of a species into a suitable, though already stable, habitat can be used to create a useful analogue. The establishment of *B. calamita* populations on reclaimed land in the Netherlands was monitored by Boomsma and Arntzen (1979). They found the colonisation of wide areas to be rapid over three or four years. In Central Europe, the same species is mainly associated with industrial wastelands and 'ruderal sites' (Necas *et al*, 1997). Some species are clearly more adept at colonising immature environments than others.

It may be useful to consider a hypothetical situation where there existed a stable optimum

habitat type, a stable optimum climate, and with with no competition. Under such perfect conditions, a species could be said to have a 'maximum potential dispersal rate'. This would be the rate of expansion possible under such hypothetical circumstances. Such conditions would of course be very unlikely, but a 'potential dispersal rate' under the existing conditions at a particular time might be a useful measure of ability to colonise a newly available habitat.

The environmental suitability, as stated earlier, is controlled by physical habitat factors, but also by climate, including annual variation and overall stability. Thus, when examining the potential of species to colonise new areas, in response to environmental change, it might be useful to introduce the concept of dispersal control. Is a particular species' expansion being controlled ultimately by its potential dispersal rate, or by extrinsic environmental factors? In other words, is its progression dispersal-limited or environment-limited? The rate of a species' dispersal could be outstripped by rapid climatic change providing new tracts of suitable habitat, faster than it can reach cross them. This is likely to be the situation at the beginning of an interglacial. During the early Holocene, it appears that palaeoenvironmental change was so fast that some plant species exhibited 'migration lags' caused by dispersal limitations. The effects of this lag cannot be distinguished in most cases from responses to gradual climatic change (Delcourt and Delcourt, 1991). Conversely, the range of a species could be restricted by the periphery of a suitable habitat. This is certain to be the greatest control during a more stable climatic period, characteristic of the main temperate part of an interglacial.

The ability of a species to immigrate into a new area must be intrinsically linked to the availability of continuous areas of suitable habitat, which form pathways or 'corridors'. Given the nature of palaeoclimatic fluctuations, such corridors may only be available for a finite period, and perhaps only for a relatively short time. The ability of faster-dispersing and less fastidious species to progress quickly will obviously be advantageous to them. The effect of time-transgressive processes such as terrestrial vegetation succession, seral succession in amphibian breeding water bodies, sea level change and climate change must also exert their own influences. For amphibians in particular, which use aquatic habitats for reproduction, some species will be more greatly affected than others by the natural succession of aquatic vegetation in breeding ponds. Size, lack or abundance of vegetation, water quality, depth and duration are factors which exercise control in different degrees to individual species. *T. cristatus* is closely dependant on well-vegetated ponds with abundant emergent aquatic plant (R. Griffiths, pers. comm.; C. Williams, pers. comm.). *T. helveticus* can tolerate much more sterile ponds, often with relatively low pH and even a degree of salinity (Frazer, 1983). Under a stabilised climate, as vegetation succession proceeds, it is likely that specialist amphibian and reptile would be able to out-compete not only the pioneers, but also the 'generalists'. In reality, however, it is probably more accurate to view the situation as a complex and dynamic interchange between all these factors. At the beginning of a temperate episode, pioneer species which require open ground (e.g. *B. calamita*) will be the earliest colonists (Boomsma and Arntzen, 1985). As vegetation succession proceeds, *B. calamita* cannot tolerate

shade and is also out-competed by other species more suited to well-vegetated habitats (T.J.C. Beebee, pers. comm., 1997). Species such as *R. dalmatina* which can inhabit woodland (Arnold and Burton, 1978; Necas *et al*, 1997) may well capitalise at this stage. Non-specialist species (e.g. *R. temporaria*)will be at the greatest advantage where habitats are discontinuous or fragmented, being able to live in the widest range of environments and disperse over a mosaic of habitats which would not be inhabitable by more specialised species.

7.3 Locations of glacial refugia

During the Pleistocene cold stages, European climatic zones would have effectively been moved a considerable distance southwards. Thus, the northern limits of most amphibians and reptiles must have been located in southern Europe. The geography of Mediterranean Europe is divided into peninsulas, and this must have split the range of many species. Some species might only have survived in one of the peninsulas. The repeated effects of Pleistocene glaciations may also have caused a considerable amount of subspeciation, as populations were separated geographically for long periods of time. The effects of isolation by the flooding of the Gibraltar Straits during the Pliocene was discussed by Busack (1986), and the fact that some extant species (e.g. *B. bufo*) live on either side suggests that they originated at least that long ago (a fact borne out in the fossil record).

Finding the likely locations of refugia, at the Devensian glacial maximum, may provide useful insights into Postglacial colonisation patterns. During glacial maxima, the more thermophilous species of the European herpetofauna would probably have been pushed south to the tips of the Mediterranean peninsulas, and some must have been restricted to Asia Minor. Cooler temperatures in northern Europe restrict amphibian breeding to the summer, whereas in southern Europe it often takes place in the winter. During glacial maxima, it is likely that the most thermophilous southern amphibians only tolerated the cool temperate climatic regimes experienced in southern peninsulae by adopting different breeding strategies, i.e. by breeding in the summer.

Much of the shallower areas of the Mediterranean, Ionean, Adriatic and Aegean Seas may also have been exposed as land during glacial maxima. As the Lateglacial climate ameliorated, some amphibian and reptile species must have returned to mainland Europe around the north of the Black Sea, and perhaps also across the Bosphorus Straits. Most of the large Mediterranean islands remained isolated even under lowered sea-levels, and some species have certainly been introduced by humans (e.g. *B. viridis* to Majorca).

The modern geographical ranges of different species can arguably be interpreted to show the likely origins of each species, and other aspects of its zoogeographical history. This has been backed up, in some cases, by other lines of evidence such as genetic characters (e.g. Thorpe, 1979, 1984). According to Zuiderwijk (1997c), *T. helveticus* had its glacial refugia in northern Spain and southern France. Likewise, *B. calamita* had its refugia in Iberia (Beebee, 1997a). The modern ranges support these assertions for both species. According to Strijbosch (1997), *C.*

austriaca originated postglacially from the 'Adriatico-Mediterranean' region of southern Europe. This is reflected in its modern range (Gasc *et al*, 1997), where it has southern strongholds in all three major peninsulae (Iberian, Appenine and Balkan). Conversely, the western species *N. maura* must have had refugia in Iberia, and the eastern species *N. tessellata* must have refuged in the Appenines, Balkans and Asia Minor. *R. lessonae* is distributed throughout the Appenine peninsula from where *R. ridibunda* is absent. It is ecologically a very similar species to *R. ridibunda* (Arnold and Burton, 1978; Gasc *et al*, 1997), and it appears there may have been competitive reasons why the ranges of these two species have remained mutually exclusive in southern areas, especially if isolation recurred during successive glaciations. Their original speciation might even have been a product of Pleistocene isolation events. In another example, the ranges of *R. dalmatina, L. viridis* and *E. longissima* (Anold and Burton, 1978) are very similar, with disjunct parts in the north which are isolated from the rest of their distributions. This is certainly the result of a Holocene contraction in the ranges of these species, which must have been formerly more widespread and continuously distributed.

From their modern range characteristics (Gasc *et al*, 1997), the locations of likely glacial refugia are proposed for each of the herpetofaunal taxa considered. These are shown in Table 7.1.

Table 7.1

S. salamandra - Iberia, Apennines, Balkans, possibly Asia Minor
T. marmoratus - Iberia
T. cristatus - Probably Apennines and Balkans
T. alpestris - South Balkans, Asia Minor, possibly southern Iberia and Apennines
T. vulgaris - Balkans, Asia Minor
T. helveticus - Iberia
B.variegata - Apennines, Balkans, Asia Minor
B. bombina - Balkans, Asia Minor/southern Russia
A. obstetricans - Iberia
P. cultripes - Southern Iberia
P. fuscus - Balkans, Asia Minor/southern Russia
P. punctatus - Iberia
B. bufo - Iberia, Apennines, Balkans, Asia Minor
B. calamita - Iberia
B. viridis - Balkans, Asia Minor, possibly Apennines
H. arborea - Apennines, Balkans, Asia minor, possibly Iberia
H. meridionalis - southern Iberia, possibly Apennines
R. temporaria - Western, central and eastern Europe, probably almost to the limits of permafrost
R. arvalis - Probably Asia Minor, southern Russia, possibly Caucasus
R. dalmatina - Apennines, Balkans, Asia minor
R. ridibunda - Balkans, Asia Minor
R. lessonae - Apennines, possibly Balkans
R. esculenta - Apennines, probably Balkans (esp. overlap between *R. ridibunda* and *R. lessonae*)
E. orbicularis - Southern Iberia, Apennines and Balkans, Asia Minor
L. viridis - Southern Apennines and Balkans, Asia Minor
L. agilis - Probably Balkans and Asia Minor
L. vivipara - Probably central and southeastern Europe, reaching close to the edge of permafrost, Caucasus, parts of Asia (Palaearctic distribution today)
P. muralis - Apennines, Balkans, possibly Iberia
A. fragilis - Southern Europe
C. viridiflavus - Apennines
E. longissima - Apennines, Balkans, Asia minor
N. natrix - Southern Europe, probably Asia Minor
N. maura - Iberia
N. tessellata - Apennines, Balkans, Asia Minor, possibly Caucasus
C. austriaca - Iberia, Apennines, Balkans, Asia Minor, possibly Caucasus
V. berus - Balkans, Asia Minor, Caucasus, parts of Asia (Palaearctic distribution today)
V. aspis - Apennines

7.4 AMS radiocarbon dating of herpetofaunal remains

It is crucial to be able to recognise true associations of faunal, archaeological and sedimentological material (i.e. real contemporaries in space and time), as opposed to apparent ones which have been brought together by taphonomic and geomorphological processes (e.g. slumping, settling, debris flow). Jacobi (1986) laboured this point in relation to human and *apparently* associated artefactual remains, and highlighted the part to be played by direct dating of evidence.

The advent of Accelerator Mass Spectrometry (AMS) radiocarbon dating has revolutionised the age determination of small organic elements which could not have been dated traditionally (Jacobi, 1986). It has also enabled the dating of individual finds, rather than their contexts, and to a large degree this has overcome the problem of uncertainty of association outlined above. Furthermore, the parallel dating of different faunal and floral remains from the same context can clarify their relationship.

Clast-supported sediments are more problematic than matrix-supported sediments as their components could easily have different ages. The fill is likely to be younger, and constant settling, reworking and addition of new matrix material are likely to cause problems. Even within matrix-supported sediments it may be essential to consider the possibility of reworking. In the case of small herpetofaunal remains, if fine and intricate features such as the neural and haemal spines of newt caudal vertebrae are well-preserved, then it is reasonable to assume that no reworking has taken place.

Acute example of such contextual problems are manifest at Three Holes Cave and Broken Cavern in the Torbryan Valley. At Three Holes, the sediments are spreads around the entrance to the cave. At Broken Cavern, the sediments are draped down the valley side outside the cave, and are combined with a complex and jumbled mass of boulders which have undoubtedly shifted repeatedly over the protracted period since they became detached. Whereas detailed and careful excavation and recording has unravelled the complex stratigraphy at these sites very satisfactorily, there still remains an element of doubt over the contemporaneity of an individual microvertebrate bone with its sedimentary context. At least one unit at Broken Cavern (Context 7 Lower) has already been shown to contain mixed assemblages (Price in Roberts, 1996).

With such considerations in mind, it becomes important to date microvertebrate remains themselves rather than relying on their contextual relationship. This has been attempted here by the application of a series of AMS radiocarbon dates, from the Oxford University Radiocarbon Accelerator Unit. This was the first time that AMS dating had been attempted on herpetofaunal remains and despite a few failed samples due to contamination and insufficient mass, age determination was surprisingly successful (P. Pettitt, pers. comm., 1996, 1997, 1998). Samples as small as c.20-30mg from Broken Cavern were able to produce meaningful results. Larger sample sizes (up to c.70mg) from Cow Cave and Kent's Cavern (Devon), Badger Cave and Bone Cave (Highland Region) also successfully yielded ages (see below). This is highly encouraging as it means that even partial anuran bones and 'doubled-up' snake and lizard bones are sufficient for

AMS dating. Unfortunately, two samples (TN 92 #252 and BRK #340) failed analysis through lack of datable carbon (P. Pettitt, pers. comm., 1997). This was probably due to their small size being just below the measurable threshold. Problems would have been compounded for the Tornewton Cave sample, as its level of radioactive carbon would probably have been too small to usefully measure anyway. Incidentally, an anuran scapula or similar bone weighs around 30mg, whereas a femur, tibiofibula or ilium (the largest anuran bones) weighs around 70-80mg. The results of the succesful determinations are detailed and discussed in Chapters 6, 8 and 9. All the ages obtained on amphiban and reptile remains appear to support the expected ages indicated by their contexts, and by other dates on associated biota (Lawson, 1995; Roberts, 1996). This is encouraging, in spite of the uncertainty arising from complex taphonomic circumstances at Torbryan and Creag nan Uamh, and hints that safe age implications can be drawn from the associated herpetofaunal elements. Moreover, the occurrence of newt vertebrae and other very fragile elements, sometimes in perfect condition (i.e. not reworked), instills confidence in the stratigraphic interpretations and the AMS results.

RADIOCARBON PLATEAUS AND CALIBRATION OF DATES

As discussed above, it is desirable that AMS dates obtained on herpetofaunal remains can be compared to dates on associated fauna. At Broken Cavern, the AMS dates on *B. calamita* of 11,080±220 ^{14}C BP (Context 21) and 10,850±90 ^{14}C BP (Context 14) are most comparable to the date of 10,950±95 ^{14}C BP on wolf bone from Context 10. Whereas Contexts 14 and 21 are believed to belong to the Lateglacial Interstadial, Context 10 is interpereted as a Lateglacial Stadial (Younger Dryas) deposit (Roberts, 1996). Not only does this appear to offer conflicting evidence, but the well-documented problem of a radiocarbon plateau at this time makes interpretation more difficult. Radiocarbon age determinations plotted against a calendar scale (obtained from dendrochronologies, varves and ice core records) demonstrate major plateaus of continuous radiocarbon age, which collectively account for at least 1,500 'lost' years since the Lateglacial (Kitagawa and van der Plicht, 1998, and references therein). This renders uncorrected dates useless as accurate chronostratigraphic markers, and other problems such as the presence of incompatible taxa with the same radiocarbon ages could be expected. Moreover, if there are any large excursions or fluctuations in palaeoclimatic trend, or major faunal changes at around this time, then it is regrettable but to be expected that they will be masked in a plateau of continuous radiocarbon age. Thus, for the Lateglacial, perhaps more than for any other period within radiocarbon range, calibration of dates becomes essential. Unfortunately, almost all of the literature deals with uncalibrated ages in radiocarbon years. Perhaps, then, the best that can be done is to quote ages 'bilingually', i.e. uncalibrated and calibrated. Calibrated dates are of little value for fitting into the existing framework of dates on fauna and flora which are uncalibrated. On the other hand, the future widespread acceptance of calibrated dates could occur if forward-thinking authors provided calibrated dates alongside traditional ages. Even the wholesale review and calibration of

all dates hitherto obtained might be a worthwhile, if lengthy exercise. Calibration might also become more 'user-friendly' if up-to-date calibration tables, in the style of traditional log tables, were available for easy reference.

7.5 Age of the Creag nan Uamh 'frog-earth' and its relationship to deposits elsewhere

Lawson (1995) described the stratigraphy of the Creag nan Uamh caves, detailing the faunal remains recovered in previous excavations and radiocarbon dates obtained. Despite a reasonably good understanding of the Middle to Late Devensian sequence of the caves, he was still unable to place a firm age on the Red Cave Earth which is still present in pockets and was once continuous in the entry chambers of all three caves. The Cave Earth consists of dolomitic limestone fragments, probably produced by thermoclastic weathering, in a reddish silty matrix (Lawson, 1995). It is most notable faunally as it contains numerous amphibian bones. Estimates of its age ranged from Lateglacial to Holocene and it is unclear whether the initiation of these deposits reflected a change in climatic and geomorphic factors. The herpetofaunal remains recovered (see Chapter 6) constitute a temperate fauna and it has been assumed by the author that the Red Cave Earth is Holocene in age. It is unlikely that such a diverse herpetofauna would have been present this far north during the Lateglacial, though at least five of these species are known from Lateglacial sites in southern Britain. Despite limited field recording in this area, all of the amphibian and reptile species recovered are thought to be present in northwest Scotland today (Arnold, 1995).

Eight AMS radiocarbon dates were requested in order to help elucidate the age of the Red Cave Earth. These comprise three dates on *R. temporaria,* two on *B. bufo,* two on *A. fragilis* and one on *V. berus*. No dates were requested on newt or lizard bones due to their minute size. Their fairly abundant occurrence within the same context as the other species to be dated, in excellent condition, suggests contemporaneity with the other species and that no reworking has taken place. Table 7.2 shows the AMS dating results.

Table 7.2.

Lab. no.	Sample	Species	Age in ^{14}C years BP
OxA-7283	Badger Cave, CNU #1001	*Rana temporaria*	3,040±40
OxA-7294	Badger Cave, CNU #1001	*Bufo bufo*	4,455±55
OxA-7292	Bone Cave, CNU #3005	*Rana temporaria*	4,785±55
OxA-7293	Bone Cave, exposure A	*Bufo bufo*	4,935±55
OxA-7297	Bone Cave, CNU #3004	*Vipera berus*	6,380±65
OxA-7295	Bone Cave, CNU #3005	*Anguis fragilis*	6,530±90
OxA-7296	Badger Cave, CNU #1001	*Anguis fragilis*	7,010±120

OxA-7291	Bone Cave, exposure A	*Rana temporaria*	7,950±70

The range of ages obtained covers almost five thousand years and clearly demonstrates prolonged accumulation of the Red Cave Earth unit. It is not clear whether accumulation was continuous and there are two gaps of over a thousand years in the series of dates, but only a much greater number of dates would help clarify this. Accumulation has almost certainly stopped, and the 'minimum age' for the top of the cave earth of c.1,000 BP suggested by Lawson (1995) is probably an underestimate.

Whether accumulation began much earlier than the oldest date is less easy to define. The inclusion of herpetofaunal remains could be intrinsically linked to the arrival of species at such a northerly location after climate ameliorated during the early Holocene. It may be significant to note that the oldest date is on *R. temporaria*, the species which would be expected as the earliest amphibian or reptile colonist as soon as land was ice free. However, the date of 7,950±70 ^{14}C BP may not represent (even approximately) the arrival of *R. temporaria* in Assynt. It is difficult to believe that it would not have had an earlier presence. As for the arrival of the other species (*B. bufo, A. fragilis* and *V. berus*), only speculation is possible. All three species were apparently present in southern England during the Lateglacial Interstadial and again in the early Holocene (see Chapter 9). It may be that northward dispersal took some 3-4,000 years after climate warmed sufficiently, particularly as it would have been determined to a certain degree by availability of suitable habitat. Nevertheless, it seems improbable that these few dates are a realistic reflection of the earliest arrival of each species. They do however show that the Red Cave Earth accumulated for a very protracted period without apparent change in composition, and perhaps in faunal content. To a large degree, this may be due to bioturbation by burrowing (Lawson, 1995).

The ages of similar 'frog-earth' deposits (a term coined by A.P. Currant, pers. comm.), of apparently Holocene age, in caves throughout Britain are poorly understood. The accumulation of large numbers of amphibian bones in these deposits (hence the name), leads to a possible conclusion that they were deposited during a wetter phase than today, when abundant breeding pools may have enabled greater preponderance of these species. If a parallel is drawn between frog -earth sites such as Pontnewydd and Milton Hill Cave, and the Creag nan Uamh frog-earth, then an age within the early and middle Holocene might be appropriate.

Summer temperatures probably reached a level similar to the thermal optimum of the Lateglacial Interstadial (i.e. similar to today), at c.9,800 BP (Lamb *et al*, 1966). During the Boreal to Atlantic phases, c.8-6,000 BP, summer temperatures in Britain are known to have been around 2°C warmer than today, with atmospheric precipitation less than today (Lamb, 1977). A steady but fluctuating decline in temperature began around 5,000 BP onwards, and by c.2,500 BP a drop of 2°C had been achieved, together with increased precipitation. Palaeoclimate had a somewhat oscillatory nature around this period. Warmer, drier conditions were resumed for much of the next

two millennia, though wetter phases were known. A warm palaeotemperature reconstruction for the period 8-5,000 BP, is corroborated by the occurrence of thermophilous species such as *E. orbicularis* in middle Holocene peats in East Anglia (Stuart, 1979), and dalmatian pelican in East Anglia and Somerset (Forbes *et al*, 1958; Northcote, 1980).

There is widespread evidence for tufa formation during the early to middle Holocene, from a wide geographical range of sites in the British Isles, e.g. Kent (Kerney *et al*, 1980), Isle of Wight (Preece, 1979), Dorset (Preece, 1980), Wiltshire (Evans *et al*, 1978), North Yorkshire (Keen, 1979), South Glamorgan (Evans *et al*, 1978), Clwyd (Maw, 1866), Grampian (Preece *et al*, 1984) and County Offaly in central Ireland (Preece and robinson, 1982). The fairly consistent age range for tufa deposition at most of these sites seems to be between c.9-5,000 BP, though a Radiocarbon date from the upper levels of the Co. Offaly tufa shows deposition was still occurring up to c.3,000 BP (Preece and Robinson, 1982). At Blashenwell in Dorset, an Early Bronze Age grave (c.4,000 BP) cut into tufa implies that deposition had ceased by then (Preece, 1980). Similarly, charred wood from a Neolithic ditch cut into tufa at Cherhill, Wiltshire, was Radiocarbon dated to 4,715±90 ^{14}C BP (BM-493) (Evans *et al*, 1978). Wood overlying a tufa in Lincolnshire was also dated to 4,046 ^{14}C BP (S.R.R.-1130) (Preece, 1980).

Tufa from the base of the Blashenwell deposits gave a Radiocarbon age (corrected for 'old' carbon) of between 9,400-8,900 ^{14}C BP (Thorpe in Preece, 1980), in agreement with Preece's (1980) biostratigraphic estimates for the initiation of tufa formation there. At Wateringbury, Kent, Kerney *et al* (1980) obtained a date of 8,470±190 ^{14}C BP (Q-1425) on wood from near the bottom of a tufa, which supported the approximate age indicated by associated pollen spectra. At Folkestone in Kent, wood fragments from organic silt directly beneath the base of the tufa gave an age of 9,960±170 ^{14}C BP (Q-1508), with dates between c.9.3 to 7.5ka BP within the tufa Kerney *et al*, 1980). Similarly, at Cwm Nash, Evans *et al* (1978) concluded that tufa began forming during the Preboreal period.

Preece (1980) discussed the possible causes of initiation and cessation of tufa deposits, claiming that linking them to an increase in precipitation during the Atlantic was untenable, as some tufas in Kent began forming during the Preboreal period (Kerney *et al*, 1980). Bury (1950) suggested that increased rainfall during the Atlantic ought to have increased slope erosion rather than lime precipitation. Instead, he proposed that the initiation of widespread tufa deposition during the early Holocene was probably in response to high temperatures combined with low precipitation. Since temperature is believed to have reached today's levels by c.9,800 BP, rising to 2^{o}C higher than today by c.8,000 BP (Lamb, 1977), this appears to be a plausible explanation and one that has not been countered. It should be noted, however, that tufa at Cherwell in Wiltshire did not start forming until c.7,000 BP, although oceanic conditions were already evident there for some time beforehand (Evans *et al*, 1978). It may be that local conditions, such as substrate and slope instability, may have been in greater control at some sites that at others, and that this affected

the timing of tufa genesis.

Bury (1950) suggested that as rainfall increased during the Atlantic phase, impermeable tufa-covered slopes would then have been able to dissipate runoff as sheet-wash, rather than being eroded by streams. The final cessation of tufa deposition (c. 5-4,000 BP) could thus have resulted from a decline in temperature, a further increase in rainfall, or both (Bury, 1950). Given that temperature is known to have declined steadily after c.5,000 BP, and that precipitation increased further after c.3,000 BP (Lamb, 1977), it seems logical that a temperature drop was almost certainly the single most important factor in terminating tufa deposition.

It appears that widespread and broadly synchronous formation of stalagmite floors, flowstones, travertines, tufas, brecciated cave earths and amphibian-bone-rich cave earths occurred throughout much of the early and middle Holocene. The occurrence of these deposits could reasonably be drawn as a parallel to these tufa deposits. Often these deposits overly unconsolidated cave earths, sometimes with archaeological or other dating control, or incorporate clastic sediments into their matrix to form a breccia. Tufaceous deposits at Broken Cavern and Three Holes Cave are associated with Neolithic archaeology i.e. c.5-4,000 BP, and overly Mesolithic layers (Roberts, 1996). Potter's Cave (Dyfed) has a thick stalagmite layer overlying Lateglacial archaeology (Lacaille and Grimes, 1955; Davies, 1989). Rogers' Cave (Herefordshire) has a Holocene tufaceous floor (Barton, 1995). Pin Hole Cave (Creswell, Derbyshire) has a travertine floor and brecciated deposits post-dating Late Upper Palaeolithic archaeology (Armstrong, 1929; Jenkinson, 1984). The adjacent Robin Hood's Cave has a stalagmite floor which was U/Th dated to c.8,350 BP (Jenkinson *et al*, 1986). A flowstone in Lower Cave, Avon, has been U/Th dated to 6,000±1,000 BP, though in this case its surface is still actively forming (A. Baker, pers. comm., 1998). The deposition of a lake marl in the Whitemoor Channel (Cheshire) took place between 7,200-8,000 BP (Johnson *et al*, 1970), and this type of deposit may be related to the same climatic conditions also.

There does seem to be abundant evidence that a group of generically similar deposits formed across the British Isles in calcareous areas, at around the same time. The range of dates from Creag nan Uamh, between c.8,000 and 3,000 BP, certainly fits well with existing chronologies from tufa deposits. Further dating of cave frog-earths would be of undoubted benefit, but this seems to be good evidence for suggesting contemporaneity, and thus similar genetic controls, for all of these deposits. The nature of the deposit forming at a particular location must undoubtedly have been dependent on local geological, sedimentological, edaphic, climatic, topographic and other factors. Though it is improbable that higher rainfall alone was responsible for initiation of tufas (Bury, 1950; Kerney *et al*, 1980), this may have been the case for frog-earths. The earliest date from the frog-earth at Creag nan Uamh (c.7,950 ^{14}C BP) is later than the early Holocene thermal optimum reached at c.9,800 BP (Lamb, 1977), and later than the initiation of some tufas (Kerney *et al*, 1980; Preece, 1980). However, it matches the onset of the wetter (and still warmer) Atlantic phase at c.8,000 BP (Lamb, 1977) invitingly well. It is therefore tentatively suggested that the discounted

theory that higher rainfall was involved in tufa initiation, might still be applicable to frog-earths. Wetter, warmer conditions could be visualised as a ready source of suitable breeding pools and amphibian expansions. The countryside being teeming with frogs and toads would surely explain their increased importance in the diet of predators, as indicated by the vast numbers of anuran bones accumulated in caves across the country. Furthermore, the youngest date from the Creag nan Uamh frog-earth (c.3,040 ^{14}C BP) matches the postulated marked decline in average temperatures after c.3,000 BP, and lies before the transition into drier conditions after c.2,300 BP (Lamb, 1977; Jones and Keen, 1993). This may be purely coincidental but it appears to suggest that the frog-earth phenomenon is linked to the prevalence of wetter conditions than are experienced in Britain today. It remains to be seen how well, and whether, the dating of other frog-earths in Britain will agree with this picture.

7.6 *Rana temporaria* in Ireland

It has been suggested that *R. temporaria* is not native to Ireland, and that it may have been introduced during Mediaeval times, or by the Normans (Wilson, 1983). The evidence seems to be that Mediaeval writings noted *R. temporaria* was absent from Ireland at that time. This is not only contradictory to the theory of an earlier Norman introduction, but also very difficult to believe biogeographically. The fauna and flora of Ireland is undoubtedly less diverse than Britain's, but the failure of the least thermophilous amphibian in Europe to colonise Ireland would require special pleading. Given that *R. temporaria* could have been present during some colder periods during the Pleistocene, except in permafrost areas, it is inconceivable that it did not immigrate during the Holocene. The presence of *T. vulgaris* and *L. vivipara* is undisputed, and it can only be concluded that *R. temporaria* was native, even if there have been human introductions in parts of eastern Ireland. The bones from Keishcorran Cave do not appear to be old, and they might only have been deposited during historical times, but it would be interesting to obtain a radiocarbon date on them. Scharff *et al* (1902) recorded 'frog' throughout sediments which probably collectively cover the Lateglacial and Holocene.

Several *R. temporaria* bones from Keishcorran Cave were submitted for microsatellite DNA analysis by T.J.C. Beebee at Sussex University, as a control sample in the analysis of Fenland bones for English Nature's *Rana lessonae* project. The analyses successfully detected DNA which appeared to match that of recent *R. temporaria*. However, it appears that small samples of subfossil bone do not contain sufficient DNA for firm conclusions to be made using current detection techniques (Beebee, 1997b).

7.7 Exotic frogs in Fenland/East Anglia, and the possible native status of *Rana lessonae*

It has long been suggested that isolated populations of the pool frog *Rana lessonae* in East Anglia,

England, are not the results of human introductions in the 19th Century, but relict natural occurrences (Bell, 1859; Wolley, 1859; Boulenger, 1884; Gadow, 1904; Fitter, 1959; Buckley, 1986; Snell, 1994; Arnold, 1995; Buckley and Snell, 1995). Local collectors took the frogs until very recently, but by 1995 only one known specimen (a male) remained (C. Snell, pers. comm., 1997). This has been 'rescued' and is currently held in captivity by C. Snell, pending the outcome of investigative work into the species' possible native status. However, before protective measures or reintroduction procedures can be employed, firm evidence of native status is needed (A. Gent, pers. comm.). If evidence is found to be sufficient, *R. lessonae* would automatically become Britain's rarest amphibian and enjoy strong legal protection. Therefore, with *R. lessonae*'s imminent extinction in sight, English Nature initiated the 'Pool frog *Rana lessonae* species recovery programme' in 1994, led by A. Gent. This has recently involved a search for subfossil evidence for the longstanding presence of *R. lessonae* in England, particularly evidence which pre-dates and thus precludes any possible Victorian introductions.

Detailed analyses of herpetofaunal remains were undertaken from ten Fenland sites (as detailed in Chapter 6.4, and Gleed-Owen, 1997e). Remains of *R. lessonae* were identified from a Middle Saxon deposit (c.1,200-1,400 BP) at Gosberton, Lincolnshire (see Figure 6.36). This provides unambiguous evidence for the former occurrence of *R. lessonae* in Britain over a wider area than had been thought, and over a longer timespan as had been suspected by many workers. It is entirely credible that *R. lessonae* reached England naturally, probably during the early Holocene, and its subfossil remains provide reasonable proof that this species should be considered a native British species. Further work is planned in order to investigate the possibility of *R. lessonae* presence at other archaeological sites, conceivably over a wider geographical area and a longer timescale.

The records of *R. arvalis/dalmatina* from Gosberton Chopdike Drove (Lincolnshire) and Terrington St. Clement (Norfolk) certainly belong to one or both of these species, and constitute the first Holocene records of either from Britain. Unfortunately, a certain specific identification has not been reached, due to the similarity between the ilia of these species. The archaeological contexts are Early and Middle Saxon, and show that these frogs were present in Britain between c.1,600-1,200 BP. Unless human introduction took place, they must have been native since a land-bridge to Europe was present. *R. arvalis* might possibly have been present during the Lateglacial in Britain, but *R. dalmatina* must have been a postglacial colonist. Its range has clearly been in decline in northern Europe, as there are disjunct populations in Denmark (Gasc *et al*, 1997).

The Fenland finds are of considerable zoogeographic interest and show that the current British herpetofauna is not entirely indicative of that which existed earlier in the Holocene. Together with the record of *E. orbicularis* from East Wretham (Stuart, 1979), it appears that earlier in the Holocene, there were at least three more species in the British native herpetofauna than there are today. Interestingly, almost all of the Pleistocene records for *R. arvalis* come from East Anglia. This is partly explained by the general concentration of Pleistocene sites in that area, but a low-

lying area of fairly continuous wetland would have been well-suited to *R. arvalis*, and damp, open woodland could have suited *R. dalmatina*. Areas of unsuitable habitat, perhaps higher and/or better drained land probably acted as effective barriers in preventing these species from reaching much of southern Britain. However, it is conceivable that during the early Holocene, with most of the North Sea bed exposed as land (Lambeck, 1995), *R. arvalis* could have reached northeast England and Scotland. It has been suggested that *R. arvalis* may even have gone unnoticed in eastern Scotland (C. Snell, pers. comm.).

As mentioned above, the identifications of *Rana* from the some of the Fenland sites have proved very difficult, particularly ilial remains, and are not conclusive in some cases. Some of the ilia have unusually thin vexillums and a deep pre-acetabular fossa. Interestingly, two sub-adult frogs from near Dundee, prepared for the reference collection (CGO 2/29 and CGO 2/30), show the same ilial characters. Their leg length was somewhat shorter than usual for *R. temporaria*, and their skin markings were similar to *R. arvalis*. The possibility that a hybrid form, or a distinct subspecies may exist in eastern Scotland, must be considered a strong possibility. If this form is evidenced in the fenland fossils, then its distribution was formerly more widespread, and included eastern England only a thousand or so years ago.

It had been hoped that the programme of microsatellite DNA analysis might be of some use in aiding identifications and clarifying lineages. The project is aimed at developing 'signatures' of recent *R. temporaria, R. arvalis* and green frogs in Britain. This would hopefully enable not only the identification of fossil remains by DNA 'fingerprinting', but also elucidate the genetic relationships between the extant species, and between different populations. Unfortunately, analysis of the *R. temporaria* ilia from the feland sites did not detect any *R. temporaria* DNA (Beebee, 1997b). The extraction of DNA from Keishcorran Cave *R. temporaria* was successful, and failure with the fenland bones was probably due to leaching by humic acids, as only 'unknown' DNA was found (Beebee, 1997b).

8 Biostratigraphy and palaeoenvironmental significance of British Quaternary herpetofaunas

The herpetofaunal data gathered so far from Quaternary sites in the British Isles is discussed. The data are summarised in Tables 8.1 and 8.2. The locations of the sites are shown in Figure 8.1. In some cases, similarities between assemblages and the recognition of apparently useful indicator species allow tentative correlations to be drawn between sites. The implications for palaeoenvironment, and in particular palaeoclimate, are considered.

Though this field is still in its relative infancy, there is sufficient evidence for the building of a provisional Pleistocene herpetostratigraphical framework. Some guidance is drawn from other biostratigraphic pointers, but the herpetofaunal data has largely been considered independently from other lines of evidence. This should provide a useful basis for comparison with, and testing against, other lines of evidence.

8.1 Early Middle Pleistocene

Background to Early Middle Pleistocene Stratigraphy

Owing to the fragmentary and localised nature of most deposits of this age, the stratigraphy of this part of the Pleistocene is far more difficult to understand than for subsequent periods. Biostratigraphy thus plays an important part in making correlations and assigning ages to deposits. It is now widely accepted that the Early Middle Pleistocene (EMP) involved several interglacial episodes, with additional temperate stages which may or may not have been of interglacial rank. The British terrestrial record is far less complete than that of its continental neighbours, and correlation of EMP deposits has so far not been possible in many cases. It is therefore appropriate to consider here the current state of knowledge in the British EMP, and its relationships with the rather more complete sequences elsewhere in northern Europe.

The Dutch record has been divided into four interglacials, somewhat ironically named Cromerian I, II, III and IV, each with a characteristic palynology (Zagwijn, 1987, 1996). Assigning ages and correlations with the deep sea record for the EMP interglacials is difficult. Zagwijn (1996) suggested that Dutch Cromerian I correlates with Stage 21, and that II, III and IV correlate with Stages 15, 13 and 11 respectively. Palaeomagnetically, the Dutch Cromerian I must be placed below the Brunhes-Matuyama boundary, probably dating it to c.750ka. Volcanic evidence dates the Cromerian IV deposits of the Urk Formation to Stage 11, c.400ka (Zagwijn, 1996). Stages 19 and 17 do not have high thermal peaks in the deep sea record (Shackleton and Opdyke, 1976), and were not associated with high sea-levels (Shackleton, 1987), and it has been argued that they are probably not represented in the Dutch 'Cromerian Complex' (Zagwijn, 1996).

In northern Germany at least six EMP temperate episodes are represented. The earliest of these probably correlates palynologically with Cromerian I, but the others cannot be matched

Table 8.1: Fossil occurrences of amphibian and reptile taxa from Quaternary sites in the British Isles. Dots represent presence of a taxon at a site. Brackets surrounding the dot mean the record is 'cf.'. Non-specific records (e.g. *Rana* sp.) are only given in the absence of a more specific record for that genus (e.g *Rana* sp. (brown frog) or *Rana temporaria*).

1 West Runton	14 Stoke Tunnel	27 Sugworth	40 Tornewton Cave	53 Pin Hole Cave	66 Pinchbeck
2 Boxgrove	15 Selsey	28 Westbury Cave	41 Badger Cave	54 Robin Hood's Cave	67 Terrington St. Clement
3 Hall's Pit	16 Little Oakley	29 Upton Warren	42 Kent's Cavern	55 Stanton Harcourt	68 West Walton
4 Barnham	17 Swanton Morley	30 Nazeing	43 Milton Hill Cave	56 Marsworth	69 Walpole St. Andrew
5 Cudmore Grove	18 East Wretham	31 Cow Cave	44 Lower Cave	57 Deeping St. James	70 Plunkett Cave
6 Beeches Pit	19 Shropham	32 Bone Cave	45 Madawg Rockshelter	58 Sutton Courtenay	71 Dermot and Grania's Bed Cave
7 Ingress Vale	20 Mundesley	33 Whitemoor Channel	46 Cathole	59 Cassington	72 Pig Cave
8 Barnfield Pit	21 Bobbitshole	34 Steetley Cave	47 Pontnewydd Cave	60 Wookey Hole	73 Hoyle's Mouth Cave
9 Purfleet	22 Happaway Cave	35 Repton	48 Broken Cavern	61 Smoo Cave	74 Little Hoyle Cave
10 Hoxne	23 Levaton Fissure	36 Carrowmore	49 Three Holes Cave	62 Coveney	75 Potter's Cave
11 Baker's Hole Pit	24 Bathford	37 Ightham Fissures	50 Torbryan Six Cave	63 Deeping St. Nicholas	
12 Itteringham	25 Tiddington	38 Netteswell	51 Denny's Hole	64 Market Deeping	
13 Harkstead	26 Barclodiad y Gawres	39 Dog Holes	52 Rogers' Cave	65 Gosberton	

Figure 8.1: Locations of sites with herpetofaunal data presented in Table 8.1.

certainly with the Dutch sequence (Grüger, 1996). Some may relate to lesser events, for example Stages 17 and 19, or the peaks during Stage 18 which are seen particularly well in Shackleton and Opdyke's (1976) core V28-239.

Since the widely-respected early accounts of the Cromer Forest-bed Formation were given by Clement Reid (1882, 1890), West Runton has been widely accepted as the type locality for the Cromerian Interglacial *sensu stricto* (West, 1980, 1996). However, there is considerable evidence to suggest that the interglacial deposits at West Runton are more complicated than once believed, and that they represent two separate temperate phases rather than one, separated by an unknown lapse of time (Preece, 1996; Turner, 1996; Zagwijn, 1996). Furthermore, some supposedly 'Cromerian' sites probably represent intermediate temperate phases. At many localities, marine transgressive deposits such as the Mundesley Clay have been assigned to Cr III, though the equivalent estuarine beds at West Runton lie unconformably over the Freshwater Bed (Turner, 1996).

West (1996) maintained that the traditional 'Cromerian' sequence (pollen zones Cr I-IV) was valid, but Zagwijn (1996) argued that interpretation of the West Runton sequence as two separate interglacials would be much more appropriate. This would also allow for better correlation with the Dutch Cromerian Complex sequence. Many British 'Cromerian' sites appear to correlate palynologically with Cr IV (Zagwijn, 1996), and are thus assumed to be correlatives of the West Runton Freshwater Bed (Cr I-II) as well. However, non-palynological biostratigraphic indicators offer strong support for the division of the West Runton sequence. At Ostend, the more evolved form of water vole, *Arvicola cantiana* is present, wheareas its primitive ancestor *Mimomys savini* is found at West Runton (Stuart, 1996; Zagwijn, 1996). This suggests that the Freshwater Bed (probably Dutch Cromerian I) is much older than the overlying marine transgressive units (Stuart, 1996). An appropriate correlation for Ostend would be Dutch Cromerian IV (Zagwijn, 1996). Also, the molluscan character of the Freshwater Bed differs from that of palynologically-similar sites such as Sidestrand. At West Runton *Bithynia troscheli* is present without *Bithynia tentaculata*, whereas at Sidestrand *Bithynia tentaculata* is found without *Bithynia troscheli* (Meijer and Preece, 1996).

Herpetofaunal assemblages

To date, five EMP herpetofaunas have been described. A herpetofauna from the West Runton Freshwater Bed (Norfolk) Substages Cr Ib-IIb consisted *T. vulgaris, B. bufo, R. arvalis, R. esculenta* or *ridibunda, R. temporaria, A. fragilis, N. natrix* and *V. berus* (Newton, 1882a; Holman *et al*, 1988; Holman, 1989a). Newton's (1882) identification of *T. cristatus* is probably mistaken as newt taxonomy has been revised significantly since that time and the illustration appears incorrect. The identification of *V. berus* is also uncertain as the original material cannot be traced (Holman *et al*, 1988). All of the West Runton herpetofauna is from the Freshwater Bed (Holman *et al*, 1988) and no remains have come from the later deposits associated with Cr III-IV.

Sparse small vertebrate material from Sugworth (Oxfordshire) included *R. arvalis* and an indeterminite salamandrid (Holman, 1987a), and cf. *N. natrix* (Stuart, 1980). Gibbard *et al* (1996) described interglacial deposits from Broomfield, Essex, which were rich in faunal and floral remains. They claimed that amphibian remains were not identifiable to species and only recorded their finds as '*Rana* sp. or *Bufo* sp.'. They postulated that the deposits may be older than the Cromerian *sensu stricto* (cf. West Runton Freshwater Bed), and proper examination of this herpetofaunal material would be of great interest.

Lister *et al* (1990) described a herpetofauna from deposits at Little Oakley (Essex), with *R. arvalis, Rana* sp./*Bufo* sp., *Emys orbicularis* and *N. natrix*. Stuart (1979) recorded a carapacial fragment of *E. orbicularis* from Westbury Cave, and a full herpetofaunal assemblage was later given by Holman (1993a), with *P. punctatus, R. temporaria, E. orbicularis, A. fragilis, C. austriaca, N. natrix* and *V. berus*. Using the complex stratigraphical scheme adopted by Bishop (1982), the total herpetofauna from Westbury actually comes from two distinct levels. The first which shall be called the 'lower herpetofauna' is from Unit 8 cf. 'Fauna 2' of Bishop (1982) and consists only of *C. austriaca* and *E. orbicularis*. The second 'upper herpetofauna' from Units 11-15 contains the remaining species, with no species common to both. Both herpetofaunas are from the 'calcareous group' and must post-date the West Runton Freshwater Bed on biostratigraphical grounds (Bishop, 1982; Stringer *et al*, 1996).

Holman (1992a) described a diverse herpetofauna from Boxgrove (West Sussex), with *T. helveticus, T. helveticus* or *vulgaris, P. fuscus, B. bufo, B. calamita, R. arvalis, R. temporaria, A. fragilis, L.* cf. *vivipara* and *N. natrix*. All of the material came from Units 4 - 6, and mostly from Unit 4c of the Upper Slindon Sands (Roberts *et al*, 1986; Holman, 1992a). Re-examination has shown some of Holman's identifications to be incorrect (Chapter 6, this volume). The record of *T. vulgaris* from marine Unit 4b is in fact *T. alpestris*, the first British fossil record for this species. One of the *T. vulgaris/helveticus* vertebrae is *T.* cf. *alpestris*, but the others are best regarded as *Triturus* sp. *P. fuscus* is correctly reported from Unit 4c, but the bone from Unit 6a is *B. calamita.* A vertebra described as *L.* cf. *vivipara* is a misidentified caudal vertebra of *A. fragilis*. None of the snake remains can be assigned to *N. natrix*. Those which are identifiable belong to *V. berus* or *Vipera* cf. *berus*, the others are Ophidia indet. These are significant changes and the herpetofauna given by Holman (1992a) should be revised accordingly. Thus the modified specific list from Boxgrove should be as follows: *T. alpestris, P. fuscus, B. bufo, B. calamita, R. temporaria, R. arvalis, A. fragilis* and *V. berus*.

Palaeoclimate and biostratigraphy

The herpetofaunas from West Runton and Sugworth indicate a well-vegetated fully interglacial environment, with no evidence that summer temperatures were any warmer than today in southern Britain. Six of the eight taxa are native to Britain today, though *R. arvalis* and *R. esculenta/ridibunda* are not. The Sugworth fish fauna is consistent with that of West Runton

(Stuart, 1982), and strong molluscan evidence suggests correlation of these two sites (Meijer & Preece, 1996). The small mammal fauna at Sugworth is larger and more indicative of a forested environment than at West Runton, but this could reflect regional biogeographical differences (Stuart, 1982) and would help explain the impoverished herpetofauna at Sugworth. The presence of *Mimomys savini* at both sites suggests an age early in the 'Cromerian Complex' (Meijer & Preece, 1996). These herpetofaunas cannot be firmly correlated with each other but they are certainly different from other (subsequent) EMP herpetofaunas.

Westbury-sub-Mendip, Little Oakley and Boxgrove are largely distinct in herpetofaunal character from the West Runton and Sugworth faunas. Both Little Oakley and the Westbury lower herpetofauna have *E. orbicularis* and Westbury also has *C. austriaca*. Neither species is present at West Runton or Sugworth and both are notable thermophiles. *E. orbicularis* indicates summer temperatures of at least 18°C and probably as high as 20°C for breeding to be successful (Degerbøl & Krog, 1951). *C. austriaca* is Britain's rarest reptile today, being restricted to a small area of southern England. *E. orbicularis* is only found in continental Europe where its range represents a great reduction from its greatest extent during the Holocene thermal maximum. The absence of frogs or any amphibians from these herpetofaunas, and the lack of other species such as *A. fragilis* and *N. natrix* which are typical of fully interglacial assemblages, is remarkable. This is particularly so for the Westbury lower herpetofauna as anuran remains normally make up the bulk of herpetofaunal assemblages from caves. Their absence could be taphonomic, but given that this is the only Pleistocene record of *C. austriaca*, such an explanation would require special pleading. The reptile faunas reflect warm interglacial conditions for Westbury Unit 8 and Little Oakley and these sites could justifiably be considered correlatives.

The upper herpetofauna at Westbury (Units 11-15) is separated stratigraphically from the lower one by deposits which produced no herpetofaunal remains and were interpreted as representing the onset of cold conditions (Bishop, 1982). This upper herpetofauna also has a fully interglacial character and, as suggested by the small mammal fauna, must represent a subsequent interglacial which might be of the same age as Boxgrove Unit 4c (Stringer *et al*, 1996). Moreover, Currant (1989) grouped the mammal faunas of the Westbury 'pink breccia' (=Unit 11) and Boxgrove Unit 4c in his 'Group 4 assemblages'. Most of the herpetofaunal species from the Westbury upper and Boxgrove herpetofaunas are distributed throughout southern Britain today. However, the records of *P. punctatus* (Westbury) and *P. fuscus* (Boxgrove) are the first and only known records for these genera in the British Pleistocene, and neither species is present in Britain today. *P. punctatus* has a southwest European range reaching north to the English Channel and east to the Alsace in France. It offers a distinctly oceanic climatic reconstruction for the Westbury upper herpetofauna. *P. fuscus* from Boxgrove on the other hand has an eastern distribution and does not overlap with the range of *P. punctatus*. *R. arvalis* is also essentially an eastern species associated with increasingly continental climates in the south of its range. The three species almost meet in the Alsace region of eastern France (Gasc *et al*, 1997). The presence of *P. fuscus* and *R.*

arvalis indicates a more continental climate for Boxgrove Unit 4c than that indicated by *P. punctatus* at Westbury. This implies that the faunas are at least partly diachronous, though they could still be from the same interglacial. *P. punctatus* is only found in Units 11 and 13 at Westbury and is absent from Units 14-15 when other temperate species were still present. Stringer *et a*l (1996) believed that Unit 11 represents the climatic optimum of an interglacial, thus the subsequent absence of *P. punctatus* may indicate increased continentality during the later stages of the interglacial. Thus, if Boxgrove Unit 4c represents the same interglacial as Westbury upper herpetofauna, it was probably deposited during a post-optimum stage and correlates with Westbury Units 14-15.

An alternative hypothesis could be employed, however. The ranges of *P. punctatus, P. fuscus* and *R. arvalis* almost meet at the French-German border and a very specific analogy could be proposed. The geographical divide between Somerset and West Sussex during the EMP could represent the division between the ranges of *P. fuscus, R. arvalis* and *P. punctatus* in northern Central Europe today. This offers the intriguing possibility of very accurate EMP climatic reconstructions of say Alsace for Westbury and the Moselle/Rhine junction for Boxgrove. In biostratigraphic terms, these herpetofaunas are unique by their inclusion of *Pelodytes* and *Pelobates*. Furthermore, they are distinct from the subsequent Barnham-type herpetofaunas by their lack of *Hyla* and *E. longissima*.

Suggested correlations

All of the above interglacial faunas can be placed with reasonable certainty before Oxygen Isotope Stage 12 (i.e. the Anglian) in the EMP, and more specific tentative correlations can be made. Caution ought to be taken before accepting systems of 'counting back' too literally, and it might be germane at this point to consider the possibility that two interglacials (e.g. Dutch Cromerian II and III) can be accommodated within one Stage. The deep sea records (Shackleton and Opdyke, 1976) show at least two distinct peaks in Stage 15, and possibly three. Having said this, there are no obvious problems with accepting the sequence offered by Zagwijn (1996).

Placing Boxgrove and the Westbury 'upper herpetofauna' at Stage 13 is in keeping with the 'vole clock' from these sites and their continental equivalents (Stuart, 1996). The Dutch equivalent would be Cromerian III (Zagwijn, 1996). Interestingly, Zagwijn's (1996) placing of the Dutch Cromerian IV at Stage 11 implies that it may correlate with British post-Anglian sites such as Barnham.

Little Oakley and the Westbury lower herpetofauna are older than Boxgrove and Westbury upper herpetofauna, and are most likely belong to Stage 15. In the Dutch sequence (Zagwijn, 1996), these sites would correlate with Cromerian II. The West Runton Freshwater Bed and Sugworth must therefore date back to at least Stage 17. Zagwijn (1996) argued that Stages 17 and 19 are not represented in the Dutch Cromerian Complex and suggested an age of Stage 21 for Cromerian I. If this is correct, then the West Runton Freshwater Bed, which correlates with

Cromerian I, is best placed at Stage 21. However, it is worth noting that the relative height of peaks in cores V28-238 and 28-239 (Shackleton and Opdyke, 1973, 1976) are not entirely matched by those in other oceanic records (e.g Bassinot *et al*, 1994).

Clearly, there is still much to learn regarding the age and correlation of EMP sites in Britain and elsewhere. It is likely that biostratigraphy, including the study of herpetofaunal assemblages, will be able to contribute significantly to the solution of existing problems.

8.2 Late Middle Pleistocene

Chronostratigraphy

In addition to the Hoxnian *sensu stricto*, there is sufficient evidence for an earlier post-Anglian interglacial and a later post-Hoxnian/pre-Ipswichian interglacial (Bridgland, 1988). These are not recent ideas: Singer *et al* (1973) tentatively suggested the existence of a post-'Anglian', pre-Hoxnian warm stage. Correlation with the continental Holsteinian interglacial is therefore not straightforward. According to Zagwijn (1996), the palynological evidence suggests that the Holsteinian was the most oceanic of the Middle and Late Pleistocene interglacials, more so than the preceding 'Cromerian IV'. On biostratigraphic and mineralogical grounds, he argued that the Cromerian IV should be placed at Stage 11 and the Holsteinian at Stage 9 (Zagwijn, 1996). The presence of two peaks in the deep sea record at Stage 9 (Shackleton and Opdyke, 1976) could theoretically accommodate both the earlier and later 'Hoxnian' temperate stages. Nevertheless, the deep trough of Stage 12 is likely to represent the 'Anglian' glaciation, and it may be most appropriate to correlate the 'earlier Hoxnian' sites with 'Cromerian IV' on the continent and place them at Stage 11.

Pre-Stage 7 assemblages

Cudmore Grove (Essex) has produced the largest herpetofauna yet identified from Britain: *T. cristatus, T. vulgaris, Hyla* sp., *B. bufo, R. arvalis, R. esculenta* or *ridibunda, R. lessonae, E. orbicularis, A. fragilis, Lacerta* sp., *E. longissima, N. natrix, N. maura* or *tessellata* and *V. berus*. The assemblage came from the largely freshwater Bed 3 of Bridgland *et al* (1988). Seven of the fourteen species are exotic. Ashton *et al* (1994) gave a similarly diverse herpetofaunal list from Barnham (Suffolk): *T. cristatus, T. helveticus, T. vulgaris, H. arborea, B. bufo, B. calamita, R. arvalis, R. temporaria, E. orbicularis, A. fragilis, E. longissima* and *N. natrix*. Holman (1994) identified a small herpetofauna from Beeches Pit, West Stow (Suffolk) with *Triturus* sp., *Rana* sp., *A. fragilis* and most notably *E. longissima*. Some herpetofaunal remains were also recovered from Dierden's Pit, Ingress Vale (close to Barnfield Pit, Swanscombe, Kent). These consist of *E. orbicularis* (Stuart, 1979), undetermined frog or toad remains (Stuart, 1982) and *N. natrix* (Holman, 1987b). The amphibian remains from Ingress Vale are as yet unidentified and further examination would be useful. These faunas have obvious affinities which are discussed below. Hoxne, Suffolk, has produced only a small herpetofauna with *B. bufo* and *N. natrix* (Holman,

1993b). From Purfleet (Essex), Holman & Clayden (1988) listed *T. cristatus, Triturus* sp., *B. bufo, R. arvalis, R. temporaria, A. fragilis* and *N.* cf. *natrix*. Holman (1987b) identified *B. bufo* from an unspecified location at Barnfield Pit, Swanscombe, but no other taxa are known from this site at present.

Biostratigraphy and palaeoclimate

The LMP herpetofaunal assemblages found so far from pre-Stage 7 sites could arguably be separated into two groups though they are not incompatible with one another. One group is represented by Cudmore Grove, Barnham, Beeches Pit and Ingress Vale and contains particularly thermophilous southern European species as well as more northerly exotics.The most notable aspect of these 'Barnham-type' herpetofaunas is the inclusion of *E. longissima* which is found at Cudmore Grove, Barnham and Beeches Pit. These are the only records of this species from Britain to date, implying the correlation of these sites and allowing their distinction from older sites such as Boxgrove and Westbury, and from Stage 7 sites. Ingress Vale has no *E. longissima* but it does have *E. orbicularis*. Therefore, since *E. orbicularis* is unknown from the Westbury upper herpetofauna, Boxgrove, Hoxne or Purfleet but is found at Cudmore Grove, this supports a tentative correlation of Ingress Vale with Cudmore Grove (and thus with Barnham and Beeches Pit). Thus it is almost certain that Cudmore Grove, Barnham, Beeches Pit, and possibly also Ingress Vale, represent the same LMP interglacial. *Hyla* is also found at Barnham and Cudmore Grove; its only other British record is from Itteringham, Norfolk (Stage 7) (Hallock *et al*, 1990; Holman, 1992b).

The second group is represented only by Hoxne and Purfleet. It is less diverse with only one exotic species (*R. arvalis*) and lacks the real thermophiles. However, as all of the species from Hoxne and Purfleet are also found at Barnham, and only *R. temporaria* is missing from Cudmore Grove, it is difficult to draw too many conclusions. There could be taphonomic or zoogeographic reasons for the absence of the major thermophiles from Hoxne and Purfleet, rather than being indicative of a cooler climate; consequently their separation from the Barnham group might not be valid. Nevertheless, the Hoxne and Purfleet herpetofaunas ostensibly imply a climate no different to that of northern England today. None of the recorded species are particularly thermophilous though the presence of *T. cristatus, A. fragilis* and *N. natrix* indicates a well-vegetated temperate environment.

The age(s) of these sites remains unresolved. The aminostratigraphy of Bowen *et al* (1989) and Bowen (1992) appears to provide a relative chronostratigraphic framework which is consistent with the oceanic Oxygen Isotope record. Two amino acid ratios on non-marine molluscs from Barnham gave values comparable to those at Swanscombe, suggesting that the deposits dated to Stage 11 around 400,000 years ago (Bowen *et al*, 1989; Ashton *et al*, 1994). Though Cudmore Grove is palynologically 'Hoxnian' (H. Roe pers. comm. to Holman *et al*, 1990), stratigraphical evidence links it specifically to earlier deposits at Clacton and Swanscombe (Bridgland *et al*,

1988). The herpetofaunal evidence supports the placing of Barnham, Cudmore Grove, Beeches Pit and Ingress Vale in a pre-Hoxnian (*sensu stricto*) position, perhaps at Stage 11, but by no means proves it. This is in keeping with the presence of thermophilous elements such as *Corbicula fluminalis* and *Macaca sylvanus* at Cudmore Grove (Bridgland *et al*, 1988).

Interestingly, Bridgland *et al* (1995) noted that *Arvicola terrestris cantiana* from Purfleet has teeth intermediate in form between those from Swanscombe and Hoxne and those from Ipswichian sites. Unfortunately, without agreement that Swanscombe and Hoxne are correlatives, this is somewhat ambiguous in its implication. Hence Purfleet could be the same age as Hoxne but it is unlikely to be older. However, and rather importantly, the thermophiles *Corbicula fluminalis* and *Macaca sylvanus* are also present at Purfleet (Preece, 1995; D. Schreve, pers. comm., 1997) and might support the correlation of Purfleet with the Barnham group. Nevertheless, Purfleet's altitude is too low for such a correlation (Bridgland, 1988). Where this leaves Hoxne is unclear.

As for Barnfield Pit, there is insufficient herpetofaunal evidence to suggest a correlation either way. Currant (1989) tentatively grouped Swanscombe with Hoxne in his 'Group 3' mammal assemblages. Bridgland (1988), however, firmly correlated Swanscombe with Cudmore Grove and the Clacton Channel, i.e. the Barnham group.

Oceanicity vs. continentality

According to the herpetofaunas, summer temperatures at the Barnham-type sites sites must have been greater than in southern Britain today, perhaps by 2 or 3°C. Holman *et al* (1990) went further and postulated that the exotic snake species from Cudmore Grove infer 'mild winter temperatures as well as high summer temperatures'. This is not necessarily so, as *E. longissima* and *N. tessellata* are distributed throughout most of eastern Europe, experiencing fully continental winters. Furthermore, in association with the thermophilous taxa at Cudmore Grove, the presence of *R. arvalis* implies a more continental climate than if it was absent from the fauna. Therefore it is most likely that the eastern-ranging *N. tessellata* is present at Cudmore Grove, rather than the western *N. maura*. Holman *et al* (1990) concluded that the herpetofaunal evidence mostly supported an oceanic interpretation of climate, and suggested a modern analogue of central or southern France. Holman (1993c) later argued that the nearest modern analogue for the Cudmore Grove herpetofauna would be Trieste in northern Italy. Based on the modern ranges of the species identified, the current author would disagree with an oceanic climate reconstruction as such.

West (1980) suggested that palynologically the Hoxnian in East Anglia showed 'greater oceanicity' than the subsequent (meaning the Ipswichian) interglacial. Holman *et al* (1990) accorded with tradition and appear to have skewed their interpretation to fit West's picture. However, the collective herpetofauna from Cudmore Grove does not indicate an oceanic climate but is in fact distinctly continental. It is more analogous to somewhere in central eastern Europe, with warmer summer temperatures than in southern Britain today, but quite likely with colder winters.

Stage 7 sites

Stuart (1979) recorded *E. orbicularis* from Selsey, West Sussex. From the same site, Holman (1992d) listed *B. bufo, B. calamita, Rana* sp. and *N. natrix*. Stoke Tunnel, Ipswich and Harkstead, both in Suffolk, have also produced *E. orbicularis* (Stuart, 1979). Itteringham in Norfolk has produced the largest Stage 7 herpetofauna with *B. bufo, H. meridionalis, R. esculenta* or *ridibunda, R. temporaria, E. orbicularis* and *N. natrix* (Hallock *et al*, 1990; Holman, 1992b). Stanton Harcourt, Oxfordshire, has produced sparse herpetofaunal remains of *T. vulgaris* or *helveticus, R. temporaria* and *R. arvalis* or *dalmatina* (Gleed-Owen, this volume). The lower channel at Marsworth in Buckinghamshire has so far produced only fragmentary remains of a brown frog *Rana* sp. (Gleed-Owen, this volume) and the Otter Stratum of Tornewton Cave, Devon, has yielded a few indeterminate toad *Bufo* sp. and frog *Rana* sp. (Gleed-Owen, 1996a, this volume).

There is some contention over the age of the Itteringham interglacial beds. Hallock *et al* (1990) tentatively assigned them on stratigraphic grounds to an Ipswichian age, but Currant (1989, 1996) is convinced that the mammalian biostratigraphy places it firmly in Stage 7. Stratigraphic and biostratigraphic evidence also convincingly suggests that Harkstead, Stoke Tunnel, Selsey and Stanton Harcourt belong to a Stage 7 interglacial (Wymer, 1985; Allen *et al*, 1992; Buckingham *et al*, 1995).

Palaeoclimate

The occurrence of *H. meridionalis* at Itteringham is the only record of this species from Britain. It has a disjunct southwest European range, reaching somewhere between the Gironde and the Loire, though its northern limit is uncertain (García París, 1997). Its presence at Itteringham demands a summer temperature 2-3°C greater than today and an oceanic climate. Unfortunately, the difficulty of identifying *Hyla* remains specifically means that this record ought to be regarded as provisional. Nevertheless, the notable absence of *R. arvalis* from Itteringham implies an oceanic or at least a 'westerly' climatic interpretation, and the Itteringham molluscs confirm the palaeotemperature estimate (Schreve, 1998). Harkstead, Stoke Tunnel, Selsey and Itteringham all have *E. orbicularis* which ranges across Iberia and southern France and can support a warm oceanic reconstruction. Non-*Emys* herpetofaunal remains were not recovered (or have not yet been described) from Harkstead or Stoke Tunnel. The thermophilous nature of these herpetofaunas is in contrast with the impoverished and sparse material recovered from some Stage 7 sites. For example, Stanton Harcourt has one exotic species, moor frog *R. arvalis* or agile frog *R. dalmatina*, but no notable thermophiles. Likewise, Marsworth and Tornewton Otter Stratum lack thermophiles though this could be owing to a taphonomic bias as so little material has been available.

It is possible that the Itteringham-type thermophilous herpetofaunas date to a warmer part of Stage 7, and that the Stanton Harcourt-type assemblages represent only a moderately warm phase. Such a subdivision of Stage 7 is accepted in the French Middle Pleistocene sequence (e.g. Andrieu

et al, 1997), and a Substage 7b global cold phase has been suggested by Andrews (1983). In Britain, Schreve (1998) has suggested subdivision on mammalian biostratigraphic grounds, correlating Bed d at Itteringham and lower beds at Aveley (both with *Crocidura* and *P. antiquus*) to the warmer Substage 7c. Upper levels at Aveley contain *M. primigenius* and cannot be Ipswichian, thus Schreve (1998) suggested correlation with the apparently less warm Substage 7a. This might also be an appropriate position for the herpetofaunas from Stanton Harcourt, Marsworth and Chislet.

8.3 Late Pleistocene (except Devensian Lateglacial)

Last (Ipswichian) Interglacial

Four sites with herpetofaunal remains of this age have been published. *E. orbicularis* was recorded from Mundesley in Norfolk (Newton, 1879; Stuart, 1979) and Bobbitshole, Ipswich in Suffolk (Stuart, 1979). Holman (1987c) identified *B. bufo, R. arvalis, R. temporaria, E. orbicularis* and *N. natrix* from Swanton Morley, Norfolk. Palynological evidence from Swanton Morley and Mundesley places these faunas at Ip Ib-IIb (Stuart, 1979; Coxon *et al*, 1980). At Shropham in Norfolk, Holman & Clayden (1990) recorded *T. vulgaris, B. bufo, R. arvalis, R. temporaria,* green frog *Rana* sp., *E. orbicularis,* cf. *L. vivipara* and *N. maura* or *tessellata*. All of these herpetofaunas have *E. orbicularis* and are compatible with each other. *N. maura* or *tessellata* has also been identified from Ipswichian deposits at Deeping St. James, Norfolk, alongside *B. bufo* and *Rana* sp. (Gleed-Owen, this volume).

As is true of the Barnham-type faunas, the sympatry of *R. arvalis* with thermophiles such as *N. maura* or *tessellata* infers continentality. Hence, the most suitable palaeoclimatic reconstruction for the last interglacial would be a fairly continental climate with summers at least 2-3°C warmer than southern Britain today but possibly with colder winters. A modern analogue of southern Germany or the Czech Republic might be appropriate. Alternatively, a more southerly climate than this (as suggested by palynological, molluscan and mammalian evidence from Ipswichian sites) would still be in keeping with the herpetofaunal reconstruction. In biostratigraphic terms, the presence of *N. maura* or *tessellata* may be of value in distinguishing between Stage 7 and Stage 5e sites.

Later Stage 5 and Middle Devensian

Later Stage 5 here is used to mean that part of Stage 5 after the Ipswichian (Substage 5e), i.e. Substages 5a-d. Comparison of the Greenland and Antarctic ice core records (Grootes *et al*, 1993; Bender *et al*, 1994) and the North Atlantic deep-ocean records (Adkins *et al*, 1997) demonstrates a series of rapidly superimposed interstadials occurring for much of the period 100-40ka BP. Obviously this makes lithostratigraphical correlation of events very difficult, and the importance of biostratigraphy is heightened. Though not as warm as the preceding Ipswichian, temperate stages

during later Stage 5 may have been as warm as the current interglacial. Adkins *et al* (1997) showed how the nature of terminations could be very rapid, perhaps within 400 years, thus it may be expected that thermophilous faunas and floras from post-Ipswichian interstadials would have been repeatedly wiped out. This would have meant renewed immigration of thermophiles in each interstadial, perhaps offering scope for biostratigraphically useful differences in faunal character.

Later Stage 5 herpetofaunas

Herpetofaunal remains are little-known from these periods and anuran material recently identified from Cassington (Oxfordshire) and the Hyaena Stratum at Tornewton Cave (Devon) provide important new data on Stage 5 and Middle Devensian anuran faunas. The herpetofaunal assemblage from Tornewton Cave Hyaena Stratum is the largest from a Stage 5 interstadial, with *B. bufo, B. calamita, R. temporaria,* cf. *L. vivipara, A. fragilis* and cf. *N. natrix* (Gleed-Owen, 1996, this volume). Stage 5 interstadial sediments at Cassington produced *B. bufo, R. temporaria* and indeterminate green frog, *Rana ridibunda, lessonae* or *esculenta* (Gleed-Owen, 1998). At Shropham (Norfolk), the post-Ipswichian 'Pocket 2' produced *R. temporaria* and *N. natrix* (Holman, 1992e).

Palaeoclimate and relative ages

By comparison with the present northerly limits of green frogs in Scandinavia and Russia, the green frog from Cassington implies a mean July temperature of at least 16°C and probably higher. From coleopteran evidence at Cassington, Maddy *et al* (1998) suggested a summer temperature of 17-18°C in keeping with the herpetofaunal reconstruction. Both the green frog and *N. natrix* would require a long enough period of summer warmth for development of larvae and incubation of eggs respectively (longer than *B. calamita* would require). These species are also more associated with well-vegetated ponds and lush meadows, than with the sparse, open heath typically preferred by *B. calamita*. It is notable that whilst these faunas indicate temperatures perhaps as warm as southern Britain today, they lack the most thermophilous elements of the Ipswichian herpetofaunas. By comparison with the Holocene herpetofaunal succession where *N. natrix* only became widespread during the middle Holocene, the presence of this species at Shropham (Pocket 2) and Tornewton Cave (Hyaena Stratum) suggests comparably interglacial conditions were experienced during later Stage 5.

Bowen (in Maddy *et al*, 1998) obtained amino acid ratios from Cassington molluscs which indicated an age intermediate between Ipswichian (Substage 5e) and Upton Warren Interstadial ratios. Maddy *et al* (1998) excluded correlation with the Chelford Interstadial at Substage 5c, and defined a new 'Cassington Interstadial' at Substage 5a. The Tornewton Cave assemblage is believed to date to a post-Ipswichian part of Stage 5 on stratigraphic and mammalian biostratigraphic grounds (Currant, 1996; Currant and Jacobi, 1997). The record of *B. calamita* from Tornewton Cave Hyaena Stratum infers a mean July temperature of at least 15°C at some

time during deposition. *B. calamita* is notably thermophilous and its distribution in Britain today very closely matches the 15°C July isotherm. The age of the Tornewton Hyaena Stratum herpetofauna could be placed at either Substage 5c or 5a. Correlation with Shropham Pocket 2 and/or Cassington is possible but cannot be proved at present.

Numerous fragmentary remains of *R. temporaria* and a few bones of *B. calamita* have been identified from Wookey Hole Hyaena Den (Gleed-Owen, this volume), but the inferred age of this herpetofaunal assemblage is somewhat ambiguous. The samples came from the basal water-lain sediments which produced an Early Devensian (Stage 4) Banwell-type large mammal fauna (Currant and Jcobi, 1997; R. Jacobi, pers. comm., 1997; A.P. Currant, pers. comm., 1998). The boundary between these deposits and the overlying cave earth, which yielded a Middle Devensian (Stage 3) Coygan-type mammal fauna (Currant and Jacobi, 1997), is not clear (A.P. Currant, pers. comm., 1998). The *R. temporaria* remains are very rolled, in keeping with the fluvial nature of the sediments, and it is likely that most if not all of them belong to Stage 4. Nevertheless, for the reasons outlined in Chapter 6.2, it is very likely that the *B. calamita* remains date to the beginning of Stage 3 (i.e. the junction of the two deposits). The record of *B. calamita* is thus considered in the Stage 3 section below.

Stage 3 (Upton Warren Interstadial)

Interstadial deposits at Sutton Courtenay (Oxfordshire) and Upton Warren (Worcestershire) have produced herpetofaunal remains of Middle Devensian age. Herpetofaunal remains from the Upton Warren type-site have not been examined recently but Stuart (1982) recorded *R. temporaria*. It is not known which part of the sequence the remains came from. A single bone of *B. calamita* is the only herpetofaunal evidence known from Sutton Courtenay. This is taphonomically remarkable, as *R. temporaria* is almost always the most frequently found amphibian species in fossil assemblages. Biostratigraphically and lithostratigraphically, it is believed that Sutton Courtenay may correlate with the Middle Devensian Upton Warren Interstadial Complex (UWIC). As stated above, it is believed that the *B. calamita* remains from Wookey Hole (Somerset) are also of this age. *R. temporaria* may also have been present, but without stricter stratigraphic control this cannot be ascertained as yet.

Palaeoclimate and age

The *B. calamita* finds at Wookey and Sutton Courtenay offer a reconstruction of at least 15°C for July temperatures. This ties in well with coleopteran data for the initial thermal optimum of the UWIC. Mutual climatic range (MCR) analyses produced a July temperature (TMAX) of 15°C for the intial thermal maximum (traditionally c.43-42ka ^{14}C BP), with a possible ceiling of 20°C at 43ka ^{14}C years BP (Coope, 1987). TMAX before and after this period was no more than 12°C which would be inhospitable to *B. calamita*. Clearly, therefore, the occurrence of *B. calamita* at

Sutton Courtenay and Wookey Hole can be tied very firmly to the short period at the beginning of the UWIC, and corroborates Coope's (1977, 1987) thermal reconstruction for this time. In Britain, *B. calamita* is today confined to coastal dunes, heaths and salt-marshes. It is a capable pioneer in newly available habitats (Boomsma & Arntzen, 1985) but is soon forced out by vegetation succession and competition with *B. bufo* (T. Beebee, pers. comm. 1997). This makes it an excellent and accurate marker of rapid climatic amelioration events. It also requires well-drained sandy soils in which to hibernate. As Sutton Courtenay and Wookey Hole are not coastal locations, the records imply a prevalence of open grassland or heath in order for *B. calamita* to immigrate there. The absence of species such as *N. natrix* from these faunas supports the view that stable interglacial conditions were not reached in the thermal optimum of the UWIC.

Bowen *et al* (1989) placed the UWIC at Substage 5a, but Currant & Jacobi (1997) and Coope *et al.* (in press) suggested a Stage 3 age. A sharp peak in the ice core curves, dated by annual layer counting to around 40ka BP (Jouzel *et al*, 1989), could certainly accommodate the thermal optimum of the UWIC. Despite doubts about Radiocarbon ages of this magnitude (Coope, 1986), this age would accord with traditional Radiocarbon ages for the UWIC thermal optimum (e.g Coope, 1977).

8.4 Devensian Lateglacial and Holocene

The herpetofaunal evidence from sites already published is presented here together with that gathered during the current project. These assemblages collectively provide an almost continuous record throughout the whole of the Lateglacial and Holocene. Table 8.2 shows the stratigraphic and chronostratigraphic positions of the assemblages, and associated dating controls where these are available, including direct AMS radiocarbon dates on amphibian and reptile remains. The combined information is synthesised as a Lateglacial and Postglacial herpetofaunal history of the British Isles.

Lateglacial Interstadial

Climatic warming at the start of the Lateglacial Interstadial (c.14.5ka calendar years BP or c.13ka ^{14}C BP) was evidently rapid (Atkinson *et al*, 1987; Johnsen *et al*, 1992). The immigration of thermophilous amphibians and reptiles would certainly have lagged behind this. The earliest herpetofaunal remains recorded from the Lateglacial in Britain are from Context 15 at Broken cavern, where *Rana* sp. (probably *R. temporaria*) was present alongside *L. vivipara* (Gleed-Owen in Roberts, 1996; Gleed-Owen, this volume). Both species have Palaearctic distributions and are Europe's most cold-tolerant amphibian and reptile respectively. The remains may pre-date the initial thermal rise at the beginning of the Lateglacial Interstadial, or may have been the first arrivals as climate ameliorated before being joined by more thermophilous species restricted by dispersal rates. The same two species are represented in Lateglacial deposits at Nazeing (Allison *et al*, 1952), but with the addition of *B. bufo* which is not certainly known from Devon caves and may have

been absent in the southwest. The Nazeing bones have not been checked, and it remains a possibility that *B. calamita* is among the toad remains, but it is interesting to speculate that the identifications are correct and that *B. calamita* did not reach southeast England during the Lateglacial. The Nazeing fauna could conceivably span a sizeable portion of time, between 13-11ka BP, and AMS dating would be of obvious benefit.

The earliest thermophilous Lateglacial Interstadial fauna from Devon is probably that from the Late Upper Palaeolithic hearth at Three Holes Cave (Context DGB), with *Bufo* sp., *R. temporaria, L. vivipara* and *A. fragilis* (Gleed-Owen in Roberts, 1996; Gleed-Owen, this volume). Several AMS dates on mammals from this layer group closely between 12.0-12.3ka ^{14}C BP (Roberts, 1996), and this age can fairly certainly be associated with the herpetofauna. Notably, the toad remains are indeterminate and either *B. bufo* or *B. calamita* could have been present.

At Broken Cavern, Lateglacial Interstadial Contexts 14 and 21 yielded *B. calamita, R. temporaria, L. vivipara, A.fragilis* and *V. berus* (Gleed-Owen in Roberts, 1996; Gleed-Owen, 1997a, this volume). It is not clear for how long this fauna was established, but the earliest dates are on *B. calamita* at 11,080±220 and 10,850±90 ^{14}C BP. These dates are clearly well after the thermal optimum of the Interstadial, rather they are almost at the end of the Interstadial. None of the remains can be tied to the thermal optimum of the Lateglacial Interstadial. This may reflect the late arrival of the herpetofauna from distant glacial refugia, for example *B. calamita* from its Iberian refugia. Alternatively, it is possible that these species were present earlier, but that their remains did not accumulate until later due to taphonomic reasons. This is a more likely explanation, especially as several taxa managed to reach as far as southwest Wales and the Wye Valley during the Lateglacial Interstadial (see below). The presence of *B. calamita*, close to the end of the Lateglacial Interstadial, must nevertheless have been associated with a July temperature of at least 15^{o}C. The presence of *V. berus* at Broken Cavern is the only record from Britain during the Lateglacial.

Torbryan Six Cave yielded only indeterminate *Rana* and *A. fragilis* from its Lateglacial Interstadial layer (Gleed-Owen, this volume). A.P. Currant (pers. comm., 1997) and A. Roberts (pers. comm., 1997) are somewhat sceptical over the presence of *A. fragilis* in Lateglacial contexts, owing to the nature of cave-entrance talus sediments and the fossorial habits of *A. fragilis*. Nevertheless, viewing the Lateglacial record of *A. fragilis* from three Devon caves as contamination would arguably be special pleading. Moreover, a direct AMS date on middle Holocene *A. fragilis* from Broken Cavern fits exactly with existing dates and archaeology from its context (see Chapter 6.2 and below). On balance, it must be considered a likelihood that the Lateglacial *A. fragilis* remains are *in situ*. If this is so (and climatically it is totally feasible), it provides the earliest record for the colonisation of this species since the last glacial maximum. Cow Cave and Kent's Cavern may have partly Lateglacial assemblages, as discussed in Chapter 6.2, but additional dating would be required to ascertain this. Their faunas are entirely compatible with the Lateglacial and early Holocene assemblages from the Torbryan caves. The absence of any newt

remains from Lateglacial contexts in the Devon Caves is worthy of mention.

Denny's Hole in Somerset yielded *B. calamita* and *R. temporaria*, indicating a similarly temperate climate as in Devon. The impoverished nature of this assemblage points towards a Lateglacial Interstadial rather than an early Holocene age. Corroborative evidence comes from Rogers' Cave in the Wye Valley (Herefordshire), Hoyle's Mouth and Potter's Cave (Dyfed) in southwest Wales, all of which have *B. calamita* in Lateglacial Interstadial contexts (Gleed-Owen, 1997b, this volume).

At Rogers' Cave, a Final Upper Palaeolithic occupation horizon, dating to c.12-11ka BP (N. Barton, pers. comm., 1998) contained *T. vulgaris/helveticus, B. bufo, B. calamita, L. vivipara* and *A. fragilis* (Gleed-Owen, this volume). This is intriguing as it appears to be the first point, geographically, where *B. bufo* and *B. calamita* can be shown to have co-existed during the Lateglacial Interstadial. Furthermore, Hoyle's Mouth Cave and Potter's Cave also produced both toad species in Lateglacial Interstadial contexts (Gleed-Owen, 1997b, this volume). Little Hoyle Cave yielded only *B. bufo* and *R. temporaria* (Gleed-Owen, 1997b, this volume), but this probably reflects taphonomic controls as there were fewer remains overall from this cave than at Hoyle's Mouth and Potter's Cave (where *B. calamita* is present in much lower proportions than *B. bufo* anyway). It is thus suggested that *B. bufo* originated from a southeasterly direction first, and *B. calamita* immigrated via the southwest of Britain. This point is discussed in more detail for *B. calamita* in Chapter 9, but it is accepted that *B. calamita* originated from Iberian refugia (Beebee, 1997a). *B. bufo* has a much more extensive range, and immigrants from southeastern (Adriatico-Mediterranean) Europe might well have reached southeast Britain first, before reaching the southwest. The lack of *B. bufo* at Denny's hole might also indicate a slightly earlier age than the southwest Wales faunas. This would in turn support an earlier arrival for *B. calamita* in Britain than the dates from Broken Cavern. Admittedly, these are speculative suggestions.

A further point of interest is the presence of *T. vulgaris* at Potter's Cave and *T. vulgaris/helveticus* at Rogers' Cave, both in Lateglacial Interstadial contexts (Gleed-Owen, 1997b, this volume). As mentioned above, there are no Lateglacial newts in the Devon caves, implying that they reached Wales by colonising from east to west. Furthermore, Rogers' Cave has *L. vivipara* and *A. fragilis* present during the Lateglacial Interstadial (Gleed-Owen, this volume), but none of the three caves in southwest Wales yielded any reptiles. This supports an east-west dispersal, presumably from southeasterly glacial refugia. Certainly, if the reptiles were present in southwest Wales, but absent from Herefordshire, it would be more difficult to argue an east-west colonisation route. Their absence from southwest Wales may also indicate that *L. vivipara* and *A. fragilis* dispersed more slowly than the amphibian species found at these sites, though both species were present in Devon at this time (see above).

Lateglacial Stadial (Younger Dryas)

During the Lateglacial Stadial (Younger Dryas), it is certain that all thermophilous amphibian and

reptile species would have become extinct. A barren, extremely cold tundra landscape is suggested by remains of reindeer, lemmings and pika from many sites in southern Britain. It must be considered a possibility that *R. temporaria* may have persisted, as today it is found up to the margins of glaciers in the Alps and Scandinavia. *L. vivipara* also reaches the high Arctic today, but neither species could have tolerated permafrost conditions. Herpetofaunal remains from undisputed Lateglacial Stadial horizons are only known from Broken Cavern. Context 10 at Broken Cavern was apparently deposited under arctic conditions (Roberts, pers. comm., 1997) and contained remains of *Rana* sp. and *A. fragilis* (Gleed-Owen, this volume). The frog is almost certainly *R. temporaria*. The presence of *A. fragilis* in an apparently 'Arctic' deposit is slightly disconcerting, although its exact age and location within the unit is unknown. Wolf bone from Context 10 was AMS dated to 10,950±95 ^{14}C BP (Roberts, 1996), closely matching the *B. calamita* age of 10,850±90 ^{14}C BP from the supposedly early Holocene Context 14 (see below). Thus, the *A. fragilis* from Context 10 could be of a very similar age to the wolf. Again, this subject is dealt with in more depth in Chapter 9, but it provokes the suggestion that climatic changes around this time were characterised by sharp fluctuations rather than a steady decline into arctic conditions.

Remains of *B. calamita* alongside *R. temporaria* from Context 11 (Gleed-Owen in Roberts, 1996; Gleed-Owen, 1996, this volume) were expected be of early Holocene age (Roberts, 1996, pers. comm., 1996). However, an AMS date of 10,420±120 ^{14}C BP on *B. calamita* suggests its presence during the Lateglacial Stadial (10,180 ^{14}C BP even at two sigma deviation). It has long been suggested that the latter half of the 'Younger Dryas' was significantly warmer than the first half (Lowe and Walker, 1980; Lowe and Gray, 1980), characterised by a 'marked thermal improvement' for the period c.10,500-10,000 BP (Lowe and Gray, 1980). There is now abundant evidence in support of this view (Isarin, 1997; see also Chapter 9). After its Lateglacial Interstadial expansion, the range of *B. calamita* would have retreated during the Younger Dryas. Nevertheless, in the European mainland it would have been better placed for a more easterly immigration into Britain. There is currently no evidence to confirm that *B. calamita* did not reach southeast England during the Lateglacial (the only site of this age is Nazeing), but this may well have been the case.

The absence of other thermophilous species from Context 11 at Broken Cavern may reflect climatic instability, or a persistence of low winter temperatures even though summer temperatures were clearly moderately warm by then. A few fragmentary remains of *R. temporaria* from Lower Cave (Avon) (Gleed-Owen, this volume) underlie a flowstone which was U-Th dated to between 5-7,000 BP (A. Baker, pers. comm., 1998). This may suggest an early Holocene age for the frog, but the absence of any other species, and the brittle and degraded nature of the remains, could indicate a Lateglacial Stadial age.

Earliest Holocene

The earliest dated Holocene assemblages are from Cow Cave and the Wolf Den at Kent's Cavern

(Devon), and Ightham Fissures (Kent). The faunas from Cow Cave and Kent's Cavern had been thought to be at least partly Lateglacial, not least because they appeared to yield mixed warm and cold small mammal assemblages (Holman, 1988; R. Jacobi, pers. comm., 1997; C. Price, pers. comm., 1997). The two herpetofaunas are essentially the same, with *B. bufo, B. calamita, R. temporaria* and *V. berus* shared by both (Holman, 1988; Gleed-Owen, this volume). The only difference being that Cow Cave had *A. fragilis* whereas Kent's Cavern had *L. vivipara.* AMS dates on *B. calamita* gave similar ages for both sites (Cow Cave: 9,270±80 ^{14}C BP; Kent's Cavern: 9,690±140 ^{14}C BP) and fill a gap in the early Holocene which is not represented in the Torbryan Caves. Due to suggestions of possible reworking at Kent's Cavern (Price, pers. comm., 1997) and Cow Cave (R. Jacobi, pers. comm., 1997), it is possible that the herpetofaunas are composite. However, *B. calamita* and the other taxa were concentrated in one discrete unit (Layer F) at Kent's Cavern, whereas the other layers had only one or two taxa present (Gleed-Owen, this volume). If reworking is a problem here, it is certainly not obvious, and the Radicoarbon age on *B. calamita* could arguably be applied to all of the taxa from Layer F.

Ightham Fissures produced the remains of *T. helveticus, B. bufo, B. calamita, R. temporaria, L. vivipara, A. fragilis, C. austriaca* and *V. berus*, in abundant concentrations (Holman, 1985). No direct dating has been carried out on the assemblage, but Holman (1985) argued that it probably dates to c.9,500 BP. *B. calamita* and *C. austriaca* are the most notable elements and neither is present in Kent today. *C. austriaca* is Britain's rarest and most thermophilous reptile, and this is its only known fossil record since the EMP (Westbury Cave). Strijbosch (1997) claimed that *C. austriaca*'s postglacial expansion originated in the Adriatico-Mediterranean region and had reached Scandinavia by 10,000 BP, though it is not clear what evidence he has. If such an early arrival in (presumably southern) Scandinavia is true, then a similarly early arrival in southeast England is possible and was evidently the case. The AMS dates on *B. calamita* from Devon support an early presence in Kent also. An arrival from southeast England would be expected, particularly as it would have been more easterly distributed in the European mainland by the early Holocene.

A largely complete skeleton of *T. helveticus* from Ightham (Holman, 1985; 1987b) represents the first Postglacial record of this species. Since there are no newt records this early from the Devon caves, its presence at Ightham may indicate an easterly route for its arrival in Britain. Early Holocene sea levels were obviously higher than during the Lateglacial Interstadial, and the land-bridge to southern England would have receded much further to the east by then (Lambeck, 1995; Wingfield, 1995). Both *B. calamita* and *T. helveticus* dispersed from southwest European glacial refugia (Beebee, 1997a; Zuiderwijk, 1997c). However, *B. calamita* was present in Devon before the beginning of the Holocene (see above), and seems to have arrived earlier than *T. helveticus*. The fact that *T. helveticus* is restricted to a 'subatlantic' distribution today (Zuiderwijk, 1997c) is probably significant. Although it reaches further north than *B. calamita* in Britain and tolerates lower summer temperatures, *T. helveticus* cannot tolerate cold continental

winters and, unlike *B. calamita*, it does not range eastwards beyond central Germany. Its later arrival in southeast England was therefore probably dependant upon amelioration in winter temperatures, associated with increased oceanicity at the beginning of the Holocene. Again, this supports the suggestion that the earlier presence of *B. calamita* at c.10.4ka BP in Devon (see above) was at a time when winters were still very cold, though summer temperatures must have been rising.

Early to Middle Holocene

Early and middle Holocene deposits at Rogers' Cave are less specific in their age (Barton, 1994; pers. comm., 1998). Layer 3 and the younger Layer 2 yielded *B. bufo, R. temporaria* and *A. fragilis* (Gleed-Owen, this volume). From nearby Madawg Rockshelter, a few bones of indeterminate Anura and *A. fragilis* (Gleed-Owen, this volume) are associated with later Mesolithic archaeology, and dates ranging between 8.7-6.6ka ^{14}C BP (Barton *et al*, 1997). It does not appear, therefore, that *B. calamita* made a Holocene appearance in the Wye Valley.

In Cheshire, the Whitemoor Channel marl yielded *T. vulgaris, T. helveticus, B. bufo* and *R. temporaria*, dated palynologically to early Holocene pollen zone V (Johnson *et al*, 1970; Holman and Stuart, 1991). This is the only dated assemblage (albeit indirectly) from northern England. Both *T. vulgaris* and *T. helveticus* are present, but none of the reptiles, nor *B. calamita* (which is found extensively along the west coast today), are represented. This is an open aquatic site, probably a life assemblage, and it is unsurprising that no reptiles are present. Several other sites in northern England have small and poorly dated herpetofaunal assemblages. In the Creswell area (Derbyshire), Steetley Cave has unidentified frog and probably *L. vivipara* (Bramwell *et al*, 1984). Pin Hole Cave and Robin Hood's Cave in the nearby gorge produced *T. vulgaris, B. bufo* and *R. temporaria* (Gleed-Owen, this volume). Dog Holes on Warton Crag (Lancashire) yielded *B. bufo, R. temporaria, A. fragilis* and *N. natrix* (Holman, 1989b). Unfortunately, none of these sites are adequately dated, though the Creswell bones are probably Mesolithic.

In Assynt, northwest Scotland, the Creag nan Uamh Caves yielded *T. helveticus, T. vulgaris/helveticus, B. bufo, R. temporaria, L. vivipara, A. fragilis* and *V. berus* (Gleed-Owen, this volume). An AMS date on *R. temporaria* from Bone Cave gave an age of 7,950±70 ^{14}C BP, perhaps relating to the initiation of Red Cave Earth. It is conceivable that *R. temporaria* did not arrive until this time, but this would demand a very protracted period for its northwards colonisation. *R. temporaria* would have been the first herpetofaunal species to begin its progression northwards as the last permafrost thawed. The development of a humid terrestrial plant cover would have been its main requirement, and an initial lack of such habitat might have been a hindrance to dispersal. The earliest date on a thermophile at Creag nan Uamh, around a thousand years later (c.7,010 ^{14}C BP), shows that *A. fragilis* had reached the neighbouring Badger Cave by this time. There is likely to have been a dispersal-limited lag time for this species to cross the length of Britain. Nevertheless, radiocarbon dates can only be seen as minimum ages for the true arrival

times of the respective species. Another AMS determination on *A. fragilis* from Bone Cave produced a result of c.6,380 ^{14}C BP and *V. berus* from Bone Cave was dated to c.6,530 ^{14}C BP. This is the earliest evidence for the occurrence of *V. berus* in Scotland, but by no means precludes the possibility of an earlier arrival. *T. helveticus, T. vulgaris/helveticus* and *L. vivipara* are consistently represented in all samples of the Red Cave Earth, but their bones are too small to date unless twenty or so were bulked. *L. vivipara* shares the same climatic tolerances as *R. temporaria*, and could have been an equally early immigrant (c.8.0ka BP or earlier; see above), provided that a humid herb cover was available. *T. helveticus* is a distinctly oceanic species and cannot tolerate continental winters. It had reached Cheshire (Whitemoor Channel) between 8.0-7.2ka BP (Holman and Stuart, 1991).

At Three Holes Cave, an assemblage with *T. helveticus, B. bufo, Rana* sp. and *A. fragilis* was present (Gleed-Owen in Roberts, 1996; Gleed-Owen, this volume) alongside Later Mesolithic artefacts, at around 6.3ka ^{14}C BP (Roberts, 1996). This is the first evidence of newt immigration to southwest Britain during postglacial times. Raised sea-levels, and a land-bridge restricted to southeast England by the early Holocene (Lambeck, 1995; Wingfield, 1995), imply an east-west colonisation routeway. This is supported by the arrival of *T. helveticus* at Ightham during the earliest Holocene. It is interesting to note that both small newt species reached Cheshire earlier than the first newt evidence from Devon.

At Three Holes, small newts, *T. helveticus* and/or *T. vulgaris* are represented in layers with Neolithic and Bronze Age archaeology (Roberts, 1996; Gleed-Owen in Roberts, 1996; Gleed-Owen, this volume). The Neolithic layer can be dated generically to between c.5.0 and 4.0ka BP (Roberts, pers. comm., 1998), and the taxa which were already present at c.6.3ka BP during the Mesolithic (Roberts, 1996) are joined by *L. vivipara* in its first appearance since the Lateglacial. *T. helveticus* also appears during the Neolithic in Broken Cavern nearby, along with *B. bufo, B. calamita, A. fragilis* and *V. berus*. This is the only middle Holocene occurrence of *B. calamita* in southwest Britain. The deposits (Contexts 8, 13 and 25) at Broken Cavern have been well-dated and provide a close grouping of ages around 4.5ka ^{14}C BP. The associated reappearances of *B. calamita* and *V. berus* are their first since the early Holocene of Cow Cave and Kent's Cavern. This might be due to a hiatus in accumulation at Broken Cavern, or local absence of the species. Forest growth during the early to Middle Holocene (Mesolithic) would not have been conducive to *B. calamita*, but there does not appear to have been any clearance during the Neolithic (Cartwright in Roberts, 1996; Price in Roberts, 1996).

During the same period in northwest Scotland, three AMS dates on *B. bufo* and *R. temporaria* gave ages of c.4,973, c.4,785 and c.4,455 ^{14}C BP (Gleed-Owen, this volume). This shows that the Red Cave Earth was still accumulating in the Creag nan Uamh caves, though it cannot be proved that the whole assemblage persisted throughout the period covered by the dates.

A cave earth at Milton Hill Cave (Somerset) produced a diverse herpetofaunal assemblage

with *T. vularis/helveticus, B. bufo, R. temporaria,* possibly *R. arvalis, A. fragilis, N. natrix* and *V. berus*, probably of early to middle Holocene age. Interestingly, *T. cristatus* has not been recorded from any of the Devon caves though it is present in the area today (Arnold, 1995).

A similar herpetofaunal assemblage is recorded from Pontnewydd Cave (Clwyd). Here, the Red Cave Earth yielded *T. cristatus, T. vulgaris, T. helveticus, B. bufo, R. temporaria, A. fragilis* and *N. natrix* (Gleed-Owen, this volume). This unit underlies the Upper Clays and Sands (Green *et al,* 1981) and is most likely to be of early to middle Holocene age, although no direct dating has been carried out on either layer. An older age for this assemblage than that of Milton Hill Cave may be unlikely, biogeographically, given that there are no other records of *T. cristatus* or *N. natrix* from anywhere in Britain to represent its expansion to North Wales. The overlying Upper Clays and Sands produced only *B. bufo* and *R. temporaria* (Gleed-Owen, but detailed analyses of this unit have not been carried out yet. It would be useful to obtain AMS dates from these units.

On the west coast of Anglesey (Gwynedd), a Megalithic tomb known as Barclodiad y Gawres contained *B. bufo, B. calamita, R. temporaria* and *N. natrix* (Pumphrey, 1956). Its Neolithic age (c.4.0-5.0ka BP) may be contemporaneous with the assemblages from Milton Hill and Pontnewydd, and is certainly comparable to the Neolithic contexts at Broken Cavern (Devon).

It is notable that in North Wales, *B. calamita* was absent at Pontnewydd, although it was present at the coastal site on Anglesey. *B. calamita* was extant along the north coast of Wales earlier this century, and it is still widespread today in Deeside and northwards along the Merseyside, Cumbria and Solway coasts (Arnold, 1995). *T. cristatus* was present at Pontnewydd, but not in the Devon or Somerset caves, and appears to have crossed central England to North Wales without reaching southwest England. This apparent lack of evidence from the west arguably implies that, like the smaller newts, it colonised from the east. Similarly, *N. natrix* reached both sites in North Wales, but reached Somerset as well, yet it is not known from the Devon caves.

Since *T. cristatus* and *N. natrix* are more demanding of mature well-vegetated ponds (for breeding and hunting, respectively), than the anurans and smaller newts, their progression northwards and westwards was probably linked to the availability of suitable habitats. This may imply that the assemblages from Milton Hill and Pontnewydd are of middle Holocene (perhaps c.4.0-7.0ka BP), rather than early Holocene age. Conversely, *V. berus* (a more xerophilous heathland species) was present in Kent and Devon at c.9,500 BP, and in northwest Scotland by c.6,500 BP (see above), yet it does not appear in Welsh cave records.

Early to middle Holocene herpetofaunal evidence from eastern England is almost unknown. The single and most celebrated find is *E. orbicularis* from peat near East Wretham, dating probably to pollen subzone VIIa, c.5.0-7.0ka BP (Newton, 1862; Stuart, 1979). *E. orbicularis* is widely reported from the middle Holocene peats of Denmark, southern Sweden and Germany (Isberg, 1929; Degerbøl and Krog, 1951; Peters, 1977) and must have enjoyed a more extensive distribution during the warmer, sunnier and perhaps more continental Holocene thermal optimum. *E. orbicularis* was probably a relatively late arrival in Britain, and since a land-bridge connected

southeast England to the continent until about 7,000 BP (Lambeck, 1995), perhaps it probably arrived after 8,000 BP.

Middle to Late Holocene

Fenland Sites

The combined records from ten Fenland sites provide a more or less continuous record of herpetofaunal assemblages for the period between 4,000-1,000 years ago, and allow some interesting comparisons with the modern herpteofauna of the area. At least seven amphibian and two reptile species were present during this period. At Gosberton (Lincolnshire), in addition to the native species found, *R. arvalis* and/or *R. dalmatina* was present during the Early and/or Middle Saxon periods (c.1,600-1,200 BP) and *R. lessonae* was present during the Middle Saxon period (c.1,400-1,200 BP) (Gleed-Owen, 1997e, this volume). *R. arvalis* was probably also present at Terrington St. Clement (Norfolk) during the Middle or Late Saxon periods (Gleed-Owen, 1997e, this volume). As these species are either extinct or not recognised as native today, these finds are of considerable zoogeographic interest, and show that the Fenland herpetofauna was formerly more diverse until quite recently. For the extant species, the subfossil herpetofaunal assemblages identified from each Fenland site reflect present day species distributions overall, but there are some noteworthy exceptions.

Late Neolithic/Bronze Age sediments at Deeping St. Nicholas (Lincolnshire) contained relatively abundant bones of *T. cristatus, B. bufo, R. temporaria* and *N. natrix*, indicating that these species were present c.4,000-2,500 BP (Gleed-Owen, 1997e, this volume). Iron Age and Roman sediments from nearby Market Deeping continue the record from c.2,500-1,600 BP with *T. cristatus, T. vulgaris, B. bufo, R. temporaria* and *N. natrix* (Gleed-Owen, 1997e, this volume). At Coveney in Cambridgeshire, an Iron Age site (c.2,500-2,000 BP) produced *T. cristatus, B. bufo, R. temporaria, A. fragilis* and *N. natrix* (Gleed-Owen, 1997e, this volume). *A. fragilis* has its nearest record today about 20km to the southeast of Coveney (Arnold, 1995), suggesting that this species has undergone at least some reduction in its distribution since the Iron Age. During the succeeding Roman period (c.2,000-1,600 BP), a few remains representing indeterminate *Bufo* and *Rana* were deposited at Gosberton Third Drove (Lincolnshire (Gleed-Owen, 1997e, this volume).

Six sites provide abundant evidence of Fenland inhabitance by newt, frog and toad species throughout the Saxon period (c.1,600-900 BP). Perhaps not unsurprisingly, no reptile remains were recovered from these former wetland sites. The most diverse assemblage is from the Early to Middle Saxon site of Gosberton Chopdike Drove, which yielded *T. vulgaris, T. helveticus, B. bufo, R. temporaria, R. arvalis/dalmatina* and *R. lessonae* (Gleed-Owen, 1997e, this volume). If *R. arvalis* is represented, it might have been present during the Lateglacial in Britain, but the notably thermophilous *R. dalmatina* and *R. lessonae* must have been postglacial colonists. Like *E. orbicularis*, the range of *R. dalmatina* has clearly declined from its optimum in northern Europe, as there are disjunct populations in Denmark (Gasc *et al*, 1997). *R. lessonae* has evidently undergone

a similar decline in southeast England. *T. vulgaris* and *T. helveticus* are notably absent from the whole Fenland area today (Arnold, 1995).

The five remaining sites of Saxon age produced only limited herpetofunal assemblages, at least partly due to the fragmentary and thus indeterminate nature of much of the material. Only *R. temporaria* was identifiable from Early Saxon deposits (c. 1,600-1,400 BP) at Pinchbeck (Lincolnshire). Middle Saxon deposits (c. 1,400-1,200 BP) at Gosberton Mornington House (Lincolnshire) and Walpole St. Andrew (Norfolk) yielded only *Bufo* sp. and *Rana* sp. Silts of Middle to Late Saxon age (c.1,400-900 BP) at West Walton (Norfolk) produced recogniseable remains of *B. bufo* and *R. temporaria*. Deposits of the same age at Terrington St. Clement (Norfolk) are more notable as alongside indeterminate *Bufo*, they yielded a probable bone of *R. arvalis* (Gleed-Owen, 1997e, this volume).

No *B. calamita* remains were found at the Fenland sites, despite the species being present today on the Norfolk and Lincolnshire coasts. This may be due to the specialised habitat preferences of *B. calamita*. During Saxon times, as today, it may have been restricted to coastal areas of these counties and did not penetrate inland. Having said this, Gadow (1904) recorded *B. calamita* from inland sites in Cambridgeshire. No remains of *L. vivipara* or *V. berus* were found at any of the sites, and neither species is common in the fens and Bedford Levels today (Arnold, 1995). Gadow (1904) reported that *V. berus* was very rare in Cambridgeshire, and that *L. vivipara* had a very local distribution. It is therefore probable that in these low-lying wetland areas, these species have always been rare, rather than having undergone a recent decline.

There is a clear correlation between the occurrence of herpetofaunal remains and the presence of stable freshwater conditions at the (formerly) coastal sites. Gosberton, Terrington St. Clement, West Walton and Walpole St. Andrew experienced marine flooding until Middle or Late Saxon times. Either through construction of sea defences, or through natural silting up of the fens, flooding then ceased at these sites (Leah and Crowson in Gurney, 1993; Trimble, 1993; T. Lane, pers. comm., 1997; D. Trimble, pers. comm., 1997). It is from this time onwards that almost all of the amphibian remains appear in the record. This is not surprising as it reflects the need for, and demonstrates the presence of, suitable breeding ponds around these localities.

Southern Britain (Non-Fenland Sites)

At Madawg Shelter in the Wye Valley, a Bronze Age context produced only indeterminate toad (Gleed-Owen, this volume), though this is likely to be *B. bufo*. Cavell Shelter adjacent to Madawg Shelter also has *A. fragilis* in a Romano-British context (c.2,000-1,500 BP) (Gleed-Owen, this volume). In Devon, Broken Cavern (Context Upper 7) records the presence of *Bufo* sp., *Rana* sp., *L. vivipara* and *A. fragilis* (Gleed-Owen in Roberts, 1996; Gleed-Owen, this volume) during Romano-British times (c.2,000-1,500 BP) (Roberts, 1996). As the *Bufo* remains are indeterminate, it is unknown whether *B. calamita* (which is absent today) had already become extinct by the Roman Period. *B. bufo* is widely distributed in Devon today (Arnold, 1995). The

remains of *A. fragilis* demonstrate its continuous presence in southwest Britain throughout the Holocene.

Records from the English Midlands are very rare, and at present are only known from historic periods. At Tiddington (Warwickshire), a Roman well produced remains of *T. vulgaris/helveticus, B. bufo* and *R. temporaria* (Holman, 1992c), and Mediaeval horizons at Repton (Derbyshire) contained abundant *B. bufo* and *R. temporaria* (Raxworthy *et al*, 1990). Archaeological records from sites similar to these must exist across much of Britain for historic and prehistoric periods. They would undoubtedly provide a valuable source of herpetofaunal data if they were to be studied.

Scotland

As there are presently only two known locations in Scotland with subfossil herpetofaunal remains recorded, the evidence from the middle to Late Holocene is scanty. One AMS date on *R. temporaria* from Badger Cave gave an age of 3,040±40 ^{14}C BP (Gleed-Owen, this volume). This demonstrates the continued accumulation of the cave earth and input of anuran remains there for a timespan of at least 5,000 years. Again, it is uncertain whether the entire assemblage recovered from the Creag nan Uamh Caves persisted until this time.

The remains of *B. bufo, R. temporaria* and *L. vivipara* from Smoo Cave on the north coast of Scotland (Gleed-Owen, this volume) provide the most recent subfossil herpetofaunal evidence from the northern end of the British mainland. These remains were recovered from a midden dating mostly to the Viking period c.1,200 BP (Pollard, 1992). A single bone of *L. vivipara* was also recovered from another deposit within the cave (Gleed-Owen, this volume), the age of which is almost certainly earlier than the midden (Gleed-Owen, 1992).

Ireland

The three caves investigated in Co. Sligo (Ireland) produced *T. vulgaris* and *R. temporaria* (Gleed-Owen, this volume). There is no dating control over these records, but their stratigraphic position suggests they are Holocene assemblages. Interestingly, several partial skeletons of *B. calamita* were recovered during the excavation of a Megalithic (c.5.0-4.0ka BP) cemetery at Carrowmore, Co. Sligo (Ove and Persson, 1980). This provides the first subfossil evidence of *B. calamita* from Ireland and proves that it was formerly more widespread than it is today. The former presence of *B. calamita* further north than its present day distribution in Kerry, may be significant to the location of land-bridges (see Chapter 9), and ties in well with predicted colonisation routes from genetic analyses (T.J.C. Beebee, pers. comm., 1998). The three amphibian species with subfossil records described here are the only three species present in Ireland today, and there is currently no evidence that additional species reached Ireland. *L. vivipara* is the only reptile native to Ireland today, but there are no subfossil records as yet. Contention over the native status of *R. temporaria* in Ireland is discussed in Chapter 7.

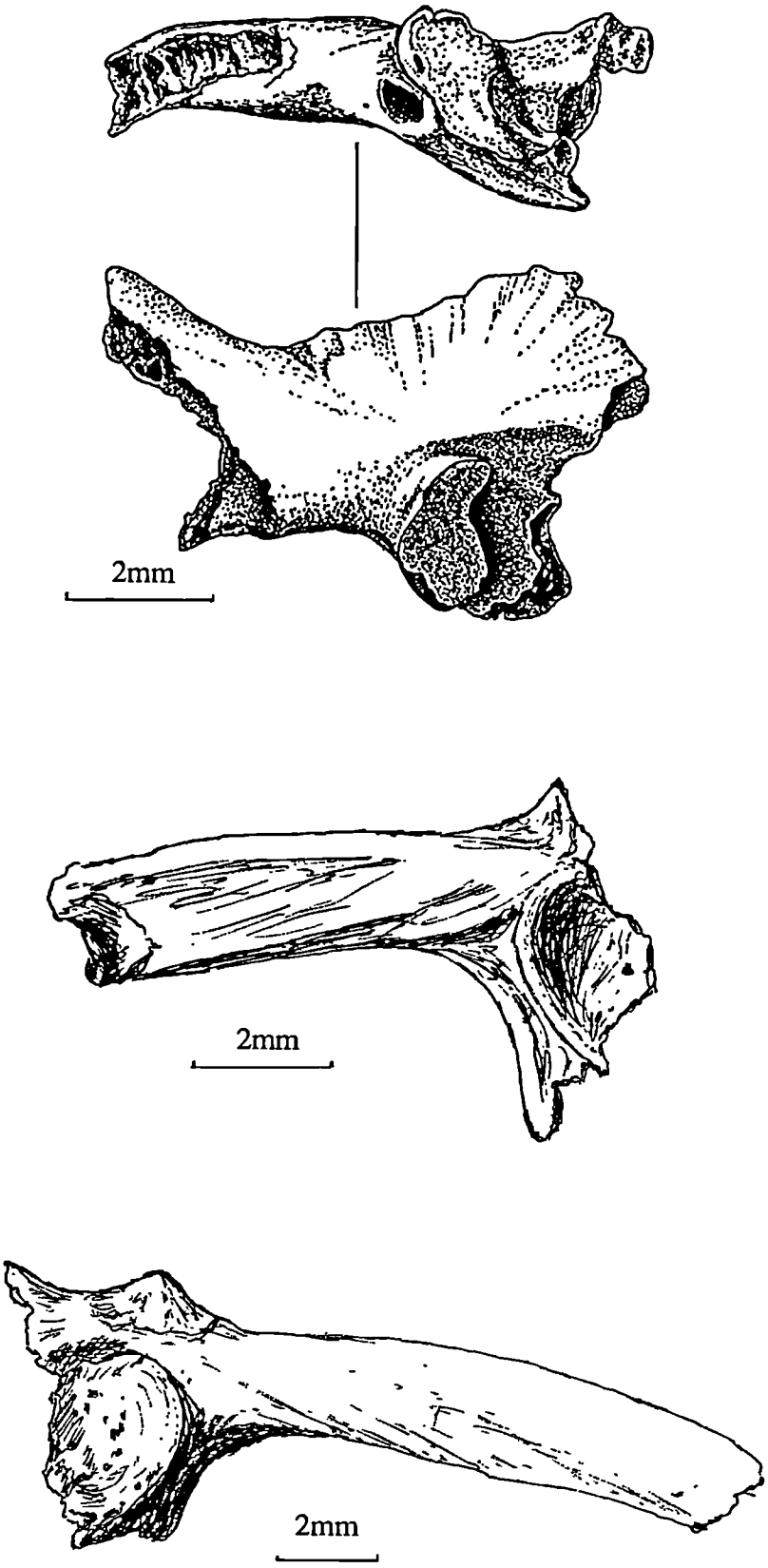


Figure 9.1: *B. calamita* bones submitted for AMS radiocarbon dating: a) right scapula from Broken Cavern, Contex 11, sample BRK #337 (OxA-6993); b) left ilium from Broken Cavern, Context 14, sample BRK #340 (failed); c right ilium from Cow Cave, NHM: R10188 (OxA-6992).

OxA 6292
Bufo calamita Broken Cavern Ctx.21
Radiocarbon Age BP 11080 ± 220
Calibrated age(s) cal BP 12992
cal BP age ranges obtained from intercepts (Method A):
minimum of cal age ranges (cal ages) maximum of cal age ranges:
one Sigma** cal BP 13216 (12992) 12779
two Sigma** cal BP 13465 (12992) 12555

OxA 6991
Bufo calamita Broken Cavern Ctx.14
Radiocarbon Age BP 10850 ± 90
Calibrated age(s) cal BP 12775
cal BP age ranges obtained from intercepts (Method A):
minimum of cal age ranges (cal ages) maximum of cal age ranges:
one Sigma** cal BP 12876 (12775) 12674
two Sigma** cal BP 12973 (12775) 12565

OxA 6993
Bufo calamita Broken Cavern Ctx.11
Radiocarbon Age BP 10420 ± 120
Calibrated age(s) cal BP 12323
cal BP age ranges obtained from intercepts (Method A):
minimum of cal age ranges (cal ages) maximum of cal age ranges:
one Sigma** cal BP 12481 (12323) 12126
two Sigma** cal BP 12619 (12323) 11841

OxA 6992
Bufo calamita Cow Cave
Radiocarbon Age BP 9270 ± 80
Calibrated age(s) cal BP 10286, 10253, 10214
cal BP age ranges obtained from intercepts (Method A):
minimum of cal age ranges (cal ages) maximum of cal age ranges:
one Sigma** cal BP 10356 (10286, 10253, 10214) 10048
two Sigma** cal BP 10439 (10286, 10253, 10214) 10034

OxA 6979
Bufo calamita Kent's Cavern
Radiocarbon Age BP 9690 ± 140
Calibrated age(s) cal BP 10945
cal BP age ranges obtained from intercepts (Method A):
minimum of cal age ranges (cal ages) maximum of cal age ranges:
one Sigma** cal BP 10996 (10945) 10556
two Sigma** cal BP 11198 (10945) 10372

Table 9.1: Results of AMS radiocarbon determinations on bones of *B. calamita*, with calibrated ages calculated using Calib 3.0 (Stuiver and Reimer, 1993).

9 *Bufo calamita* in the Late Pleistocene and Holocene

9.1 Introduction

As discussed in earlier chapters, in Britain *B. calamita* is at the northwestern limit of its range. It has a sporadic distribution (see Figure 3.19), closely related to favourable habitats: sandy heaths in the south, and coastal dunes and salt-marshes elsewhere (Boulenger, 1897-8; Beebee, 1983; Beebee, 1997a). Such a scattered distribution must have involved a formerly more continuous occurrence. The timing and routes by which *B. calamita* colonised Britain and southwest Ireland have been discussed, but without conclusion (Beebee, 1978; 1981; 1984; Walters, 1981a; 1981b; Wilkinson, 1988; Yalden, 1980; 1981; 1982). The recovery of *B. calamita* remains from a number of sites in Devensian Lateglacial contexts, is of great interest. There are implications for palaeotemperature, zoogeography and land-bridges to the continent.

9.2 AMS radiocarbon dating of Lateglacial and early Holocene records

Five AMS radiocarbon determinations have been carried out by Oxford University Radiocarbon Accelerator Unit on *B. calamita* remains from four sites in Devon. This is the first occasion that AMS dating has been attempted on amphibian remains in Britain, and possibly in the world. An initial sample was submitted from Context 21 of Broken Cavern, as the layer was believed to be Lateglacial on sedimentological grounds. Furthermore, a previous date on mammal bone from Context 21 had given an age of c.11,380 BP (Roberts, 1996). Figure 9.1 shows three of the bones submitted for dating.

The problem of radiocarbon plateaus makes correlation of Lateglacial events and records difficult. A radiocarbon age of c.10,000 years is now believed to be equivalent to around 11,500 ice core years. The ice core records are reliably accurate and comparable within 1% to real sidereal years (Alley *et al*, 1993), therefore biostratigraphic data can usefully be compared with them, using calibrated radiocarbon dates. The calibration curves produced by Stuiver and Reimer (1993) and their predecessors use dendrochronologies as a standard 'chronometer' and allow correction for plateau effects. Nevertheless, the biostratigraphic literature deals almost exclusively with uncalibrated dates, in radiocarbon years and cannot be directly compared to absolute chronologies from ice cores. Kitagawa and van der Plicht (1998) discussed the many complications and potential pitfalls of any calibration system. Admittedly the use of even calibrated radiocarbon dates is always open to some speculation regarding their accuracy.

The two partial scapulae of *B. calamita* submitted from sample BRK 500 of Context 21, gave an age of 11,080±220 BP (OxA-6292). This figure was calibrated using 'CALIB 3.0' (Stuiver and Reimer, 1993), and produced a date of 12,992 cal BP. This provides direct dated evidence of the Lateglacial arrival of the species in southwest Britain. On the strength of this date, four other

samples were submitted, from Broken Cavern, the Wolf's Den of Kent's Cavern, and Cow Cave. Two partial sacra, from sample BRK 243 of Context 14 at Broken Cavern, gave an age of 10,850±90 BP (OxA-6991), and a calibrated date of 12,775 cal BP. A right scapula (Figure 9.2), from sample BRK 337 of Context 11, gave an age of 10,420±120 BP (OxA-6993), and a calibrated date of 12,323 cal BP. Additional un-dated records of *B. calamita* have been identified from Rogers' Cave (Herefordshire), Hoyle's Mouth and Potter's Cave (Dyfed), and these are also believed to be in Lateglacial contexts (Aldhouse-Green, pers. comm., 1996; Green and Walker, 1991; Roberts, pers. comm., 1996).

One *B. calamita* ilium from Cow Cave (BMNH R10183) was also submitted for AMS radiocarbon dating. The ilium was from Layer IV, the only horizon with *B. calamita* present (Holman, 1988). The determination gave an age of 9,270±70 ^{14}C BP (OxA-6992). This converts to a median calibrated date of 10,253 cal BP, and even at a two sigma deviation the oldest possible date is 10,439 ^{14}C BP. An ilium from Sample F of the Wolf's Den, Kent's Cavern, gave an age of 9,690±140 ^{14}C BP (OxA-6979) and a calibrated age of 10,945 cal BP. The dates are shown in Table 9.1. Unless specified otherwise, the dates discussed below are uncalibrated.

9.3 Lateglacial climate and *Bufo calamita*

The Devensian Lateglacial is a well-researched chronozone, yet its complexities are far from being resolved. The Lateglacial is taken to mean the period from c.13-10,000 ^{14}C BP. This includes a mainly temperate episode of interstadial rank, c.13-11,000 ^{14}C BP, followed by a largely cold episode c.11-10,000 ^{14}C BP known internationally as the Younger Dryas (Mangerud *et al*, 1974). Evidence of the Younger Dryas cold event is recognised in most northern hemisphere terrestrial, oceanic and ice core records. The nature of the preceding phase(s), and the finer detail of the Younger Dryas are not as easily correlated across geographic regions. It is almost certain, in fact, that all events are diachronous, at least to some degree.

Traditionally, the temperate part of the Lateglacial in Scandinavia consisted of the Bølling and Allerød Interstadials, divided by a short cooling known as the Older Dryas (Mangerud et al, 1974). The Bølling-Allerød Interstadial will be referred to here as the Lateglacial Interstadial. In Britain, the evidence of an Older Dryas cooling is far from distinct, and the Lateglacial Interstadial is more or less considered to as a continuous episode. Currant (1987) hinted that an Older Dryas-type cooling may be represented by the presence of saiga antelope in Mendip Caves, and in West Yorkshire, Keen *et al* (1988) may have registered a short cooling in molluscan terms. Temperature reconstructions using the Mutual Climatic Range method, applied to Coleoptera, show that climate warmed abruptly, c.13,000 ^{14}C BP (Atkinson *et al*, 1987). Using Swedish varve chronology, Björk and Möller (1987) placed the onset of climatic amelioration at 12,700 BP. Hammarlund and Keen (1994), using molluscan evidence from southern Sweden, suggested a pronounced warming

at c.12,400 ^{14}C BP. A rapid initial warming is supported by molluscan, palynological and coleopteran evidence from many northwest European sites (Atkinson *et al*, 1989; Coope and Lemdahl, 1995; Keen *et al*, 1988; Walker *et al*, 1994), and is well documented in the Greenland ice core records (e.g. Johnsen *et al*, 1992). In agreement with the Greenland ice core, the British beetle record shows that the initial thermal peak just after 12,500 ^{14}C BP was the highest, followed by a progressive decline until climate became somewhat unstable c.11,000 ^{14}C BP, just before the onset of the Younger Dryas (Atkinson *et al*, 1987). A similar pattern is seen in the record for South Sweden and Denmark (Berglund *et al*, 1994).

At Three Holes Cave, *B. bufo, R. temporaria, L. vivipara* and *A. fragilis* are recorded from the 'DGB' context, dated to 12,260 ^{14}C BP (Roberts, 1996). *A. fragilis* appears to be restricted at its northern limits today, by length and depth of winter temperatures (Cabela, 1997); reptiles enter hibernation much earlier, and leave much later than amphibians. Arguably, its presence in Three Holes Cave at c.12,260 ^{14}C BP, and apparent absence from later deposits (with dated *B. calamita*) at Broken Cavern, support the notion that the Lateglacial Interstadial was warmest at the beginning. Progressively worsening winters and, equally importantly, shortening summers may well have caused *A. fragilis*' extinction before that of *B. calamita*.

Two *B. calamita* dates apparently fall at or close to the beginning of the Younger Dryas. Admittedly a two sigma deviation on 11,080±220 ^{14}C BP would place it within the latter half of the interstadial (11,520 ^{14}C BP), but 10,850±90 ^{14}C BP would be no older than 11,030 ^{14}C BP. The presence of *B. calamita* at these times is a sure indication that mean July temperatures were still attaining at least 15^{o}C. The breeding cycle takes as little as four weeks (Beebee, 1979), and theoretically only one month needs to reach 15^{o}C for successful metamorphosis. As *B. calamita* typically lives for 5 to 10 years (highest recorded age is 15 years: Frazer, 1983), this temperature need not be attained every year to avoid extinction. Nevertheless, evidence of *B. calamita* can be taken as a firm indication of minimum mean temperatures for the warmest month reaching 15^{o}C, at least in some years. Thus, although July temperatures at c.11,080 ^{14}C BP and c.10,850 ^{14}C BP must still have been warm, a marked decline in winter temperatures, as indicated by coleopteran evidence (Atkinson *et al*, 1987; Coope and Lemdahl, 1995), would still be possible.

B. calamita can survive cold continental winters, and it seems entirely plausible that the progressive cooling evidenced by Coleoptera may have taken the form of increased continentality. In addition, the apparent absence of *A. fragilis* at 10,850 ^{14}C BP may have been due to worsening winter temperatures, and perhaps shortened summers. A high seasonal temperature gradient may have been enhanced by astronomical factors also. During the Early Holocene, the earth was at perihelion during the Northern Hemisphere summer (Yu and Harrison, 1995). As a result, summer insolation was 8% greater than it is now, and winter insolation was 8% less (Berger, 1978).

Interestingly, Coope and Lemdahl (1995) gave a beetle record at c.10,900 ^{14}C BP which indicated a TMAX (temperature of the warmest month, taken to be July) of between 10-16^{o}C; Atkinson *et al* (1987) noted a TMIN (coldest month) of c.-5 to -18^{o}C for the same period.

The Younger Dryas has traditionally been placed between c.11-10,000 ^{14}C BP (Mangerud *et al*, 1974). Van Geel *et al* (1989) placed it more specifically between 10,950-10,150 ^{14}C BP, on dated palynological grounds. Peteet (1992), however, suggested a duration in both Europe and North America of 10,600-10,000 ^{14}C BP based palynostratigraphically on AMS dates, but this is in contrast with most data. The *B. calamita* date at c.10,850 ^{14}C BP may suggest a slightly later start than this, perhaps explained by the highly oscillatory nature of climatic fluctuations (which are evidenced in the ice cores: Alley *et al*, 1993) at this time. The fluctuations around the start of the Younger Dryas appear to have been in the order of 3-4^{o}C (Dansgaard *et al*, 1989). If there were short-term fluctuations between c.10,950-10,850 ^{14}C BP, causing regional extinction of *B. calamita*, this would require enough time for recolonisation by 10,850 ^{14}C BP. As mentioned earlier, this date could be as old as 11,030 ^{14}C BP at a two sigma deviation. This may be a more realistic interpretation in this case.

The fine resolution of the ice core ^{18}O record provides the most reliable representation of palaeoclimatic changes, and its chronology is probably closer to real time than any other records. Though there are some concerns over disturbed stratification, the cryo-chronology from layer-counting is believed to approximate reasonably well to calendar years (Grootes *et al*, 1993; Johnsen *et al*, 1992). The Greenland data show that climatic deterioration at the start of the Younger Dryas, and amelioration at its end, was abrupt (Alley *et al*, 1993; Dansgaard *et al*, 1989; Grootes *et al*, 1993; Johnsen *et al*, 1992). The Summit and Dye 3 ice cores indicate a sharp decline into the Younger Dryas at c.12,500 BP, but this was preceeded by a short cold phase ('Interstadial 1b'), beginning c.13,000 BP (Dansgaard *et al*, 1993; Johnsen *et al*, 1992). There is also a small but discernable peak in the dust record from the Dye 3 ice core at this time (Dansgaard *et al*, 1989), presumably relating to increased atmospheric dust circulation.

The *B. calamita* dates calibrated using CALIB 3.0 (Stuiver and Reimer, 1993) allow speculation regarding their correlation with the ice core records. The median calibrated *B. calamita* date of 12,992 cal BP, at one sigma deviation (see Table 9.1), could be in keeping with a cooling after this time, or alternatively the oldest of the three suggested dates (13,216 cal BP) might be more appropriate. The median 12,775 cal BP appears to fall within the 1b cooling, though the younger 12,674 cal BP date would post-date it. If the ice core chronology is accurate, then there are no real problems with fitting the *B. calamita* dates into it, but of course the relative fallibility of radiometric dating prevents any definitive statements.

From various lines of evidence (Atkinson *et al*, 1987; Berglund *et al*, 1994; Björck and Möller, 1987; Dansgaard *et al*, 1989; Grootes *et al*, 1993; Isarin, 1997; Johnsen *et al*, 1992), it is

clear that the first half of the Younger Dryas was considerably colder than the second. For the first phase, Isarin (1997) reconstructed minimum mean July isotherms, using the distribution of thermophilous plant taxa, particularly *Typha latifolia*. The isotherms have a distinctly longitudinal orientation, and for a zone including southern Britain, minimum mean July temperatures for the first phase were estimated at 12-13°C. Coope and Lemdahl (1995) have no data for the first phase of the Younger Dryas, suggesting that Atkinson *et al*'s (1987) curve was estimated for this period, and that maximum and minimum temperatures between c.10,900-10,500 14C BP cannot be estimated from British beetle evidence. From Swedish beetles, TMAX for this period is between 9-13°C, and from Polish beetles it is 8-14°C (Coope and Lemdahl, 1995). Reconstructed temperatures from multi-proxy evidence suggest that mean temperatures for the coldest month, during the first phase of the Younger Dryas, was between -15 and -25°C, with discontinuous permafrost in southern Britain (Isarin, 1997), compared with -6°C and -30°C from coleopteran evidence alone (Atkinson *et al*, 1987).

The Younger Dryas is also recognised as a major phase of dune formation due to renewed aeolian activity, and a general increase in storminess and atmospheric circulation rates (Dansgaard *et al*, 1989; Isarin *et al*, 1997). There is a sharp increase in dust content of the Dye 3 ice core at this time (Dansgaard *et al*, 1989), and in the Netherlands extensive river dune formation took place, though only remodelling of existing dunes was seen in Poland (Isarin *et al*, 1997). At Broken Cavern, a loess deposit (Context 10) probably relates to aeolian activity during the thermal minimum. This would support the assertion that glacial conditions during the Younger Dryas were accompanied by increased storminess and atmospheric dust circulation (Dansgaard *et al*, 1989). *B. calamita* is absent from this layer at Broken Cavern, with *R. temporaria* and *L. vivipara* being the only herpetofaunal species present. Both *R. temporaria* and *L. vivipara* reach the High Arctic today (Gasc *et al*, 1997) and may well have lived in southern Britain during the coldest part of the Younger Dryas. During this period, *B. calamita* could not have persisted in Britain, and its geographical range must have retreated to continental Europe. Isarin's (1997) reconstructed 15°C July isotherm for the first phase of the Younger Dryas lies across mid-France. It is generally accepted that *B. calamita* spread post-glacially from an Iberian refuge (Beebee, 1997), probably along a coastal corridor (Gleed-Owen, 1997a). Thus it is likely that the northern limit of *B. calamita*'s range lay somewhere between the Loire and Gironde Estuaries.

For the second phase of the Younger Dryas, the British beetle record between 10,500-10,000 ^{14}C BP offers a TMAX of between 9-13°C, whereas the southern Swedish record rises from c.10°C to c.15°C over this 500-year period (Coope and Lemdahl, 1995). Dated palyno-stratigraphic evidence from southeast Sweden also shows that by c.10,500 ^{14}C BP, an open birch and pine woodland had developed, and by 10,000 ^{14}C BP this had developed into closed woodland (Björk and Möller, 1987). Isarin's (1997) reconstruction from thermophilous plants

suggested minimum mean July temperatures were 1-2°C higher than for the first phase of the Younger Dryas. For southern Britain this was between 13-15°C, and judging from the isotherm distribution (Isarin, 1997: Figure 4.7), July means for southwest England were c.14-15°C. The presence of *B. calamita* in southwest England at 10,420 ^{14}C BP agrees with a suggested amelioration beginning at around 10,550 ^{14}C BP, but implies that TMAX reached 15°C at this early stage. This may be in conflict with coleopteran and botanical lines of evidence, but it could also be interpreted as an indication of climatic fluctuation at this time. For *B. calamita* to have re-immigrated into southwest England by 10,420 ^{14}C BP, it must have progressed some 6-700km since the worst of the Younger Dryas first phase. The mid-Younger Dryas amelioration in the ice core record (e.g. Johnsen *et al*, 1992) was rapid, but not as abrupt as in the preceding deterioration. It levelled out somewhat at c.10,500 ^{14}C BP, and by this time mean temperatures must have already been close to the estimates for the subsequent centuries. Nevertheless, the arrival of *B. calamita* by 10,420 ^{14}C BP seems to indicate very fast dispersal rates, in the order of 2-3km/yr. There are no direct measurements of linear dispersal rates for *B. calamita*, but such an estimate is not incredible.

At the end of the Younger Dryas, i.e. at the transition with the Holocene, the ice cores reveal a rapid termination (Alley *et al*, 1993; Dansgaard *et al*, 1993; Johnsen *et al*, 1992). There is strong evidence for a sharp rise of around 7°C within 50 years (Dansgaard *et al*, 1989), and possibly less than 20 years (Alley *et al*, 1993). Björck *et al* (1996) placed the Younger Dryas-Preboreal boundary at 11,450-11,390±80 BP, based on corrected and synchronized dencrochronologies. The end of the associated radiocarbon plateau was at about 11,200 dendro-years (Björk *et al*, 1996). The calibrated date for the 10,420 ^{14}C BP *B. calamita* record is 12,323 cal BP, which is clearly before the end of the Younger Dryas. Even at a two-sigma deviation, the youngest possible date is 11,841 cal BP.

9.4 Holocene records

The uncalibrated dates on *B. calamita* gave ages of 9270 ^{14}C BP from Cow Cave, and 9,690 ^{14}C BP at Kent's Cavern Wolf Den. The calibrated ages are 10,253 cal BP and 10,945 cal BP respectively. Even at a two-sigma deviation, the oldest possible date is 11,198 cal BP for Kent's Cavern. Using Björk *et al*'s (1996) 11,450-11,390±80 cal BP dendro-based age for the Younger Dryas termination, both of these *B. calamita* dates clearly indicate a Postglacial presence. *B. calamita* evidently colonised Cow Cave and Kent's Cavern in the Early Holocene, but from the two dates acquired so far, there is no way of telling if there was an earlier presence as at Broken Cavern. *A. fragilis* was also present at Kent's Cavern in the same context as the dated *B. calamita* remains. At Broken Cavern, *A. fragilis* was present during the Lateglacial Interstadial, but not the Early Holocene and did not reappear there until the Middle Holocene. This could be due to

taphonomic controls at either site. Whatever the case, there is clear evidence that *B. calamita* was present during the earliest part of the Holocene.

Björck *et al* (1996, 1997) identified a short (c.150-year) post-Younger Dryas cooling which they termed the 'Preboreal Oscillation', ending at c.11,000 calendar years BP. This cooling is evident in decreasing $\partial^{18}O$ values in the GRIP, GISP2 and three other Greenland ice cores, but the associated drop in temperature is unlikely to have been significant. Interestingly, the calibrated date for *B. calamita* at Kent's Cavern is 10,945 cal BP. This appears to be just after the Preboreal Oscillationt. At a two-sigma deviation (see Table 9.1) it could be placed within the cooling, but this is a less likely interpretation.

Whatever the relationship of the Kent's Cavern *B. calamita* record with the Preboreal cooling of Björck *et al* (1996), its amplitude is unlikely to have affected *B. calamita* adversely. The remains from Broken Cavern dated to 10,420 ^{14}C BP (12,323 cal BP) indicate that *B. calamita* was present during the latter part of the Younger Dryas, and Early Holocene temperatures were undoubtedly above 15^{o}C. The Cow Cave and Kent's Cavern dates show that *B. calamita* could have persisted for at least another 1,000 ^{14}C years since its Younger Dryas presence. Even accepting two-sigma error margins for the calibrated dates (Table 9.1), the difference in age between the Broken Cavern late-Younger Dryas *B. calamita* record (11,841 cal BP) and the Kent's Cavern record (11,198 cal BP) is at least 643 calendar years. The implications for *B. calamita*'s dispersal northwards are discussed later.

'*B. calamita*' was recorded from Holocene deposits in the Whitemoor Channel (Bosley, East Cheshire) by Holman and Stuart (1991). Upon re-examination of this material, all of the toad bones were found to belong in fact *B. bufo* (Gleed-Owen, 1997a), and this record should be considered incorrect. The herpetofauna from the Ightham Fissure (Kent) is believed to be Early Holocene (Holman, 1985), and included abundant *B. calamita* bones. The identifications have been checked and are accepted as correct. There were no stratigraphic details for this site, though the herpetofaunal remains were believed to come from upper layers of the sequence (Holman, 1985), rather than from the bulk of the deposits which span much of the Devensian (Newton, 1894). *B. calamita* was recorded from presumably Holocene deposits on Anglesey (Pumphrey, 1956), but this material has not been traced and the record cannot be checked. Newton's (1917) *B. calamita* record from the Creag nan Uamh caves (Assynt) remains doubtful. A further record from Denny's Hole (Somerset) described in Chapter 6 may be Lateglacial or Early Holocene.

B. calamita was recorded in apparent association with Mesolithic archaeology in Anglesey (Pumphrey, 1956). This material is now lost, and record cannot be checked, but the presence of *N. natrix* at the site would suggest a Holocene date. Remains of *B. calamita* were reliably recorded from a Megalithic cemetery in Sligo, Ireland; their age is unknown, but is presumably Holocene, and may even be recent (Ove and Persson, 1980).

9.5 Implications for land-bridges and colonisation routes

It is not feasible that viable populations of *B. calamita* existed around the British Isles for the duration of the last glaciation. At the glacial maximum, its range was probably reduced to a northwest African and Iberian refuge, from which it subsequently recolonised northwest Europe. Even in Iberia, during the much cooler climate of the last glacial maximum, it must have been restricted to favourably sandy habitats with open vegetation, as it is in the north of its range today. It seems most likely that colonisation took place along a coastal corridor, probably beginning its progression northward from the first stages of climatic amelioration in the Lateglacial Interstadial. The physical environment along the western continental margin at this time would probably have suited *B. calamita*: a low coastal plain with salt marshes and dunefields. *B. calamita* can breed in the shallowest of pools, and can tolerate brackish water (Beebee, 1979; Johnsen, 1946). As discussed previously, it readily colonises newly drained, unvegetated areas as they become available (Boomsma and Arntzen, 1985).

With a low enough sea level, a continuous band of coastal plain, from Iberia to the British Isles, could have provided a corridor for northward migration. The idea of a land link between Iberia and the British Isles may also be the only explanation for the enigmatic 'Lusitanian' elements of some western faunas and floras. During the Lateglacial, a wide land-bridge must have existed around the Celtic Sea (including much of the English Channel), and a link to southern Ireland must have existed. Sea level data for this period (Devoy, 1995; Fairbanks *et al*, 1989; Lambeck, 1995; 1996; Walker *et al*, 1994; Wingfield, 1995) offer a conflicting picture. Lambeck's (1996) glacio-hydro-isostatic model suggests that a land-bridge existed across the Irish Sea, between 18-14,000 ^{14}C BP, but not after this time, though a connection from Cornwall to northwest France still reached the Celtic Sea. In contrast, Wingfield's (1995) 'peak forebulge' model suggests that a land-bridge was exposed across the St. George's Channel at 11,000 ^{14}C BP. The land-bridge may have been up to 60km wide, and elevated to 15m. It moved progressively northwards until it was breached at around 9,500 ^{14}C BP (Wingfield, 1995). An earlier land-bridge, at say 15-13,000 ^{14}C BP, would have involved a more elevated forebulge, and a lower mean sea level, especially as lag-time for crustal subsidence is several thousand years after deglaciation (Wingfield, 1995). Mitchell (1960) also raised the point that trans-Irish Sea ridges may also have been significantly hydroisostatically depressed.

The dated evidence shows that *B. calamita* had reached southwest Britain by 11,080 ^{14}C BP. Both Lambeck's (1996) and Wingfield's (1995) models allow the immigration of *B. calamita* along a westerly route, crossing directly from Brittany to Devon. The palaeocoast maps show that the Severn Estuary was dry throughout the Lateglacial. *B. calamita* could have reached South Wales, the Wye Valley and Somerset, using a coastal route around Devon and Cornwall.

The presence of *B. calamita* in Ireland today is less easily explained. Two main possibilities have previously been considered: an Early Holocene immigration via a land-bridge, or a recent

human introduction. Beebee (1984) suggested that the Irish *B. calamita* arrived via a more westerly route than the British populations, before any fossil evidence had arisen to suggest a Lateglacial colonisation in southwest Britain. There is still no certain evidence to prove *B. calamita*'s long-term residence in Ireland, and any theories are conjectural. Human introduction, as an explanation, is discounted as a possibility here. The Lusitanian elements of the Irish fauna and flora have similarly inexplicable distributions, but human introduction is not seriously considered a likely explanation for these.

Given that dated evidence proves a Lateglacial arrival in southwest England, it might be suggested that the Kerry populations (and Sligo fossil remains?) were the result of a Lateglacial immigration. Lambeck's (1996) model does not allow for such a Lateglacial or Holocene crossing to southwest Ireland, but Wingfield's (1995) does. If *B. calamita* arrived in Ireland during the Lateglacial Interstadial, it must have endured the Younger Dryas, despite the fact that it must have become extinct in southwest England. This seems unlikely.

Alternatively, if *B. calamita* failed to reach Ireland during the Lateglacial, or did so and subsequently became extinct in the Younger Dryas, then a post-Younger Dryas immigration must have taken place. As *B. calamita* seems to have been present at 10,420 ^{14}C BP in Devon, it is interesting to speculate that it may have progressed to Ireland shortly after this time. Wingfield's (1995) map for 10,000 ^{14}C BP indicates a relatively wide (c.30km) connection from northwest Wales to Ireland, but by 9,500 ^{14}C BP, it was probably drowned. This may have been sufficient time for the expansion of *B. calamita* across the exposed coastal plains of southwest England and Wales. If it was already expanding its range before 10,000 ^{14}C BP in Devon, then a period of at least 500 years was available to reach Ireland.

The modern distribution of *B. calamita* in Britain is difficult to explain by traditional ideas. Disjunct populations on the Merseyside, Lancashire, Cumbria and the Solway coasts show no historical connection to those in southern England. Populations scattered along the dune systems of the Sefton coast are of particular interest as these sites also support *L. agilis* today, at its most northerly natural extent in Britain (Arnold, 1995). Beebee (1978) suggested 'heathland corridors', opened up by mid-Holocene forest clearance, allowed *B. calamita* to expand its range. However, the restriction of *B. calamita* to coastal areas in the west of Britain lends support to the idea that its expansion was along a coastal corridor which is now submerged. Historical records of populations in North Wales (Arnold, 1995), and fossil remains from Anglesey (Pumphrey, 1956), fill in some of the gaps along the way. It has also been suggested that a 'reverse colonisation' may have taken place from Ireland to northwest England (Gleed-Owen, 1997d), via the last remaining land-bridge at 9,750 BP proposed by Wingfield (1995). If *B. calamita* was present in Sligo (Ove and Persson, 1980), then it is conceivable that it was more widely distributed around Ireland than has previously been imagined. However, as dated evidence suggests that *B. calamita* had returned to Devon by 10,420 ^{14}C BP, there would certainly have been enough time, before sea levels attained their

maximum extent, for *B. calamita* to progress from Devon and Cornwall, along a sandy coastal corridor to the Solway.

Yalden (1980) suggested that the modern dune systems along the west coast of Britain are probably relatively young, perhaps having formed within the last 3,000 years. Dune sands at Formby Point on the Sefton coast were dated by optical luminescence to around 3000 BP, but there was certainly considerable aeolian activity before this (Pye *et al*, 1995). The widespread Shirdley Hill Sands of the Sefton coast probably originated from several phases of aeolian accumulation and reworking during the Early and Middle Holocene, and perhaps as early as Lateglacial times (Pye *et al*, 1995; Tooley, 1990). During the Lateglacial and Early Holocene, many areas of now-submerged littoral and estuarine sediments would have been exposed due to low sea levels. Even if the dunes of Devon, Cornwall, Glamorgan, West Wales and Anglesey today may not have been present since the Early Holocene, similar systems probably did exist. There is no need for a cross-country dispersal during the Early Holocene, as suggested by Yalden (1980), or during the Middle Holocene, as suggested by Beebee (1978). A continuous belt of dunes, estuarine salt-marshes and low coastal plains very probably existed during the Early Holocene, whilst sea-levels were still low. This would have provided an ideal corridor for the dispersal of the 'pioneer-opportunist' *B. calamita*, and most probably also *L. agilis*. The circumstantial evidence (fossil, historical and extant) for the Postglacial distribution of *B. calamita* in Devon, Gwynedd, Anglesey, Clwyd, Merseyside, Lancashire, Cumbria and around the Solway Estuary could support this theory.

The east coast populations probably also dispersed along a coastal route. Beebee (1978) envisaged a mid-Holocene dispersal, through heathland corridors opened up by Neolithic forest clearance. As Yalden (1980) pointed out, the vegetational history does not support this theory. However, in contrast to the west coast, the distribution of *B. calamita* in more inland areas around southeast England does infer penetration away from the coast. This may have been via the Thames valley, or across dry heathlands which later became forested. The East Anglian and Lincolnshire populations are mostly associated with coastal dunes, as on the west coast. A number of historical records of extinct populations (Arnold, 1995) in Norfolk, Cambridgeshire and Suffolk indicate that *B. calamita* did also extend inland. These records are mostly in the fenlands and broads, and *B. calamita* could easily have reached these areas during the Early Holocene. None of the ten fossil assemblages from Fenland sites studied here produced any *B. calamita* remains, even though the species must have been present a some point along the Norfolk and Lincolnshire coast, in order to found today's populations. This supports the suggestion that on the east coast it was restricted then, as it is today, to sandy coastal habitats.

9.6 Microsatellite DNA analysis of modern *Bufo calamita* populations

Microsatellite DNA analyses by T.J.C. Beebee (University of Sussex) are currently examining the genetic relationships between the various British, Irish and mainland European populations of *B.*

populations of *B. calamita*. These analyses should help elucidate the geographical origins of the modern populations, the routes by which they colonised each area, and timing of their isolation from one another. Preliminary results have not yet been published, but a few details have kindly been released very recently (Beebee, pers. comm, 1998). These results appear to have strong implications for the discussions above, and a number of salient points are worth mentioning here: 1) The British east coast populations are genetically very different from the west coast ones, so much so that they imply two different founder stocks reaching Britain; 2) The Cumbrian populations are closer to the Kerry ones than they are to the Merseyside ones, strongly supporting the traditional northern land-bridge to Ireland; 3) The 'genetic tree topography', and computer-based analyses of genetic vs. geographical distances for the west coast British populations allow prediction of the likely colonisation routes from Iberia and locations of 'splits'; 4) A preliminary 'molecular clock' has been created for *B. calamita*, and it should be possible to compare this with known climatic and geographical factors for the Lateglacial and Holocene.

9.7 Pioneer status during later Stage 5 and Middle Devensian Stage 3

B. calamita has been termed a 'pioneer-opportunist', able to expand its range into areas of suitable habitat which become available (Boomsma and Arntzen, 1985). During its Lateglacial and Early Holocene expansion, it was one of the earliest amphibian immigrants in the British Isles, despite it being the most thermophilous species. It has since declined because of habitat loss, and probably due to competition with *B. bufo* (Beebee, 1978, pers. comm., 1997). Shrub invasion into an area occupied by *B. calamita* causes rapid decline: a situation which has recently been observed in dune-slacks of northwest England (Beebee, pers. comm.). *B. calamita* cannot persist while vegetation succession proceeds, but differs from most other amphibians in that it can inhabit sparsely vegetated habitats, typically with xerophytic and sclerophyllous herbage.

The presence of *B. calamita* in the Hyaena Den at Wookey Hole, the Hyaena Stratum of Tornewton Cave and riverine deposits at Sutton Courtenay could suggest contemporaneity of these sites, but there may have been more than one Early or Middle Devensian immigration. Mammal remains suggest that the Hyaena Stratum at Tornewton Cave dates to a temperate part of Stage 5, perhaps Stage 5c (A.P. Currant, pers. comm. 1997). Currant and Jacobi (1997) considered interstadial faunas of this period to be pre-Devensian, i.e a later part of the Last interglacial after the Ipswichian *sensu stricto*. Coope (1977), on the other hand, considered interstadial sites such as Chelford to be Early Devensian. This period will be termed later Stage 5 here.

The mammal faunas associated with Wookey Hole and Sutton Courtenay are of the 'Coygan -type', which Currant and Jacobi (1997) attributed to the Middle Devensian (Stage 3). This would place these sites in the traditional age range of the Upton Warren Interstadial Complex, bounded by radiocarbon dates to c.42-25ka ^{14}C BP, which may or may not be useful in the correlation of Middle Devensian sites. The short thermal optimum at c.43ka ^{14}C BP was followed by a relatively sharp decline (Coope, 1977). There is clear evidence in the ice core records (e.g. Jouzel *et al*,

1989) for a sharp thermal amelioration during Stage 3, which may well accommodate Upton Warren-type sites.

There are no Last Interglacial records of *B. calamita*. The beginning of the Last Interglacial was characterised by a rapid rise in temperature, considerably warmer than the current climate in Britain, closely followed by an equally fast immigration of thermophilous tree species (Stuart, 1976). It is likely that eustatic sea level rise was also rapid, and isolation from the continent would have been early. These factors may have conspired against the successful immigration of *B. calamita*. If it did immigrate, it may not have been widespread. The absence of humans and horses from Stage 5e lends support to the idea of a rapid sea-level rise at the end of Stage 6, resulting in early isolation from the continent (Sutcliffe, 1995).

By analogy with the Lateglacial arrival of *B. calamita* in Britain, remains of *B. calamita* from latter Stage 5 and Middle Devensian interstadial sites, in the absence of fully interglacial herpetofaunas, provide a similar interpretation. *B. calamita* seems to be useful as a biostratigraphic indicator of periods where rapidly ameliorating climate outstripped vegetation succession. This may be linked to the persistence or return of cold winters, after summer temperatures have risen.

During the Ipswichian (Substage 5e), the initial amelioration of climate may have been fast, but vegetation immigration and succession appears to have kept pace with it, preventing the immigration of *B. calamita*. The latter part of the Ipswichian saw increased continentality (Stuart, 1976), with a decline in winter temperatures preceding the decline in summer temperatures experienced at the end of the interglacial. During the Lateglacial Interstadial, a similar situation appears to have existed, though on a shorter timescale. An initial warming, followed by declining winter temperatures, maintained an open vegetation cover, but allowed *B. calamita* to colonise southwest Britain. By analogy, a similar climatic character probably prevailed during a latter Stage 5 Interstadial, in which *B. calamita* also successfully colonised Britain.

There is strong sedimentological evidence from the Channel Islands that sea levels were lowered by at least by 5m soon after Substage 5e, and that sand dunes developed (Keen *et al*, 1995). From dating of marine terraces, it appears that only a 20m sea level drop had occurred by Substages 5c and 5a, but from the deep oceanic (benthic foraminiferal) record a 70m drop is implied though the latter may not be tenable (Shackleton, 1987). Pedological evidence indicates that Substage 5d saw a decline towards a dry sub-arctic climate, succeeded by warm and cold phases in Substages 5c-a, during which sea level continued to fall progressively (Keen *et al*, 1995). *B. calamita* could have dispersed northwards during either Substage 5c or 5a (or unrecognised shorter fluctuations), via the same western coastal route as postulated above for the Lateglacial. Clearly, colonisation would have been more likely as sea levels became lower. For this reason, it is more likely that the Tornewton Hyaena Stratum dates to Substage 5a than 5c. A palaeoclimatic reconstruction for the Early Devensian interstadial when *B. calamita* arrived at Tornewton Cave, would point towards a rapid rise in summer temperatures to at least 15°C. Winter temperatures may still have been relatively cold, or could have declined progressively.

Thus, vegetation is likely to have remained sparse and conducive to the expansion of *B. calamita.*

The evidence of a green frog (*R. ridibunda, lessonae* or *esculenta*) at Cassington, and *N. natrix* in post-5e deposits at Shropham, indicate reasonably long periods of summer warmth, probably with slightly higher July temperatures than indicated at Tornewton. A relatively stable episode of continental climate might therefore be an appropriate reconstruction for these sites. Coope (1977) suggested that climate during the 'Chelford Interstadial' was not as warm as today, and was moderately continental. It is possible that one or two of the herpetofaunas described here date to the thermal maximum of the 'Chelford Interstadial', but it seems unlikely that they are synchronous. These taxa imply a well-vegetated environment of fully interglacial rank, comparable to the Holocene. *B. calamita* at Tornewton implies a more sparsely vegetated landscape, with a temperate summer climate, but not necessarily as warm as that suggested at Shropham and Cassington. These differences could be within the clinal variation across southern Britain today, but they could also suggest diachroneity of the faunas. They could have occupied one or more of a number of temperate phases during a latter part of Stage 5 or even Stage 4. The detailed ice core record (e.g. Jouzel *et al*, 1989) seems to indicate many more sharp climatic fluctuations between 100-40ka BP than have previously been imagined. Maddy *et al* (1998) suggested a Substage 5a age for Cassington. Deciduous arboreal pollen, beetle, molluscan and fish faunal evidence there points towards a climate no less warm than southern Sweden today. This is entirely in keeping with the climatic reconstruction from the green frog at Cassington, whose northern limits today are also in southern Sweden.

The molluscan evidence at Sutton Courtenay, in the same stratigraphic level as *B. calamita*, indicates a more temperate climate than the overlying 'cool' assemblage. The overlying gravels contains a Coygan-type (Currant and Jacobi, 1997) mammal assemblage with mammoth, woolly rhino and hyaena. As *B. calamita* can be viewed as a pioneer species, the absence of any other amphibian or reptile species at Sutton Courtenay is strong evidence for a shorter warm episode than the earlier interstadial(s) evidenced at Tornewton, Cassington and Shropham. As is the case at Lateglacial Interstadial sites, the reconstruction offered by coleopteran remains from the UWIC maximum is supported by *B. calamita* at Sutton Courtenay. Coope (1977) suggested that for a short period, perhaps only 1,000 years, temperatures were 'rather warmer' than today, with a fairly oceanic character. Interestingly, R. Jacobi (pers. comm., 1997) has noted that two other Coygan-type faunas (Isleworth and Tattershall) are associated with thermophilous UWIC faunas. The mammal fauna of the Wookey Hole Hyaena Den indicates a Stage 3 (Middle Devensian) age for this site also (Currant and Jacobi, 1997; Jacobi, pers. comm., 1997). Again, the inclusion of *B. calamita* in an otherwise impoverished herpetofauna, leads to the same conclusion as at Sutton Courtenay, making correlation of these sites with the thermal maximum of the UWIC very plausible. It would be interesting to see if the Upton Warren type-site remains, with *R. temporaria* mentioned by Stuart (1982), included any *B. calamita.*

10 Concluding remarks and recommendations for future work

It was stated at the outset, that the study of Quaternary herpetofaunal remains from the British Isles is in its infancy. Although this project has advanced the state of knowledge considerably, and has applied fossil herpetofaunal data in ways which have not been carried out before, there is still a vast amount of work yet to be done. When compared with other lines of Quaternary palaeontology such as the study of fossil mammals, molluscs and flora, the amount of palaeoherpetological data that has been gathered is still very small.

Over four-and-a-half years, this project has more than doubled the volume of data gathered over the previous 140 years. In addition to the existing published herpetofaunal assemblages discussed, forty-one new sites/assemblages have been examined, and four published sites have been critically re-examined. This has considerably increased our knowledge, particularly of Late Quaternary herpetofaunas. It is hoped that this project proves that fossil herpetofaunal remains can be identified to a taxonomic level which permits palaeoecological interpretations from individual species. The results have also demonstrated that fossil assemblages have important biostratigraphic applications. They can also aid the understanding of other topics such as the biogeography and recent history of the British herpetofauna, and have unquestionable potential for other fields such as conservation. Finally, it is intended that this work can form the basis of future work, not least by providing ecological accounts of the likely species to be encountered (Chapter 2), and by setting out the diagnostic criteria by which their remains can be identified (Chapter 5).

This is an appropriate point at which to make some suggestions for future work in the Quaternary palaeoherpetology of the British Isles:

1) The taxonomy of fossil remains. The reference collection gathered so far is incomplete, and would be greatly benefited by the addition of a comprehensive range of specimens for each species. Primarily, it lacks species of *Bombina, Pelobates, Pelodytes, Hyla, Rana, Lacerta, Podarcis, Coluber, Elaphe, Natrix* and *Vipera*. Much further comparative osteological study is required for these species, in order to maximise the full potential of the fossil record.
2) Many important sites, undoubtedly with herpetofaunal assemblages in many cases, have not yet been studied. It ought to be a priority that existing collections, mainly in museums, should be surveyed and the herpetofaunal material described.
3) After re-appraisal of some of J.A. Holman's identifications, the re-examination of some other assemblages would seem prudent. This has not been possible so far, due to material being unavailable, but should be a priority in due course.
4) Areas in which the application of herpetofaunal assemblages show a good deal of potential are:
   i) Palaeoenvironmental reconstruction and correlation of Middle Pleistocene interglacial sites.
   ii) The recognition and distinction of interstadials during later Stage 5 and the Early to Middle Devensian.

iii) Climatic changes during the Lateglacial and Holocene.

iv) Biogeography, land-bridges and colonisation routes.

5) The dating of many more herpetofaunal assemblages, particularly by AMS radiocarbon, would be of obvious benefit. Very few dates exist at present, and there is scope for sizeable applications to be made in the immediate future.

6) Mapping of palaeodistributions. As more data is gathered, particularly for the last 13,000 years or so, it should be possible to map colonisation and distribution of individual species in dated 'time-slices', albeit it on a more modest scale than is possible for other taxonomic groups.

7) The value of applying data from subfossil herpetofaunal assemblages to other fields, such as conservation and genetic studies, has been proven here. Such collaborations should be pursued in the future.

8) Very little is known of Irish fossil herpetofaunas, and this would seem to be an area which is seriously in need of further work, particularly in view of its biogeographic importance.

Acknowledgements

I express my greatest thanks to my parents, Richard and Cathie Gleed-Owen, who have given continuous support, encouragement and understanding throughout the four-and-a-half years I have spent on this project, despite the fact that at times it seemed like an endless task! I would also like to thank all of my friends, family and colleagues everywhere. These have been priceless times!

I owe particular thanks to my supervisors - David Keen, Andy Currant and Bob Jones - may their interest in (palaeo)herpetology continue to grow! My studentship was funded by the School of Natural and Environmental Sciences, Coventry University. David Smith deserves particular thanks for ensuring continued financial support throughout the project. NERC funded AMS radiocarbon dates. A small grant was received from the Quaternary Research Association. Further fiscal contributions from my parents and Grandad (with his recent but keen interest in palaeoherpetology!) are acknowledged. I am also very grateful to Christine Buckingham and Kate Scott for several happy seasons digging at Stanton Harcourt - it was this that gave me the inspiration to do a PhD!

Many people have contributed in many ways to this project, particularly by providing me with dead amphibians and reptiles, skeletons, samples and fossil material, but also by much valuable discussion and friendship: Umberto Albarella, Stephen Aldhouse-Green, Pim Arntzen, David Astley, Andy Baker, Nick Barton, Trevor Beebee, David Bird, Mark Bodycote, Lee Brady, Julian Brown, John Buckley, Jim Campbell, Stewart Campbell, Brian Chambers, Sandra Chapman, Sue Charlesworth, John Clayden, Jan Clemons, Russell Coope, Pete Coxon, Anne de la Vega, Mike Field, Jim Foster, Tony Gent, Richard Griffiths, Dave Gurney, Tim Halliday, Terry Hardaker, Steven Hewitt, Al Holman, Colin Howes, Howard Inns, Brian Irving, Roger Jacobi, Paul Joslin, Liza Keane, Sarah Laming, Tom Lane, Tom Langton, Tim Lawson, Adrian Lister, R.J. Macrae, John Merry, Sally Moyes, Pete Murphy, Mike Nicholls, Jane O'Dell, Simon Parfitt, Paul Pettitt, Betty Platenberg, Tony Pollard, Cath Price, Chris Proctor, Paul Richards, Anne Riddell, Ali Roberts, Zbynek Rocek, Paul Rooney, Borja Sanchiz, Ana Cristina Pinto Llona, Dale Sergeantson, Danielle Schreve, Alex Scott, Katherine Selby, Don Sharp, Charles Snell, Tony Stuart, Zbigniew Szyndlar, Dale Trimble, Georg Waldmann, Elizabeth Walker, John Walker, Mike Walker, Martin Warren, James Wells, John Wilkinson, Clare Williams, Derek Yalden.

Christine Lovering and Christine Dawson spent many hours taking SEM micrographs which have been such an important part of this project. Elizabeth Turner provided laboratory facilities most efficiently, despite the unsavoury nature of my preparatory work! Cartographic, technical, secretarial and computer support has been given throughout by the thoroughly indispensible Lorne Elliott, Shirley Addleton, Michelle Walton, Joan James, Sheila Blackford and Gillian West. Thanks also to the other Geography staff and University people I've had pleasant dealings with over the years.

References:

Adkins, J.F., Boyle, E.A., Keigwin, Ll. and Cortijo, E. 1997. Variability of the North Atlantic thermohaline circulation during the last interglacial period. *Nature*, 390, 154-156.

Albarella, U. 1997. *The Iron Age animal bone excavated in 1991 from Outgang Road, Market Deeping (MAD 91), Lincolnshire.* Report from Ancient Monuments Laboratory, English Heritage.

Allen, L.G., Gibbard, P.L., Pettit, M.E., Preece, R.C. and Robinson, E. 1996. Late Pleistocene interglacial deposits at Pennington Marshes, Lymington, Hampshire, southern England. *Proceedings of the Geologists' Association* , 107, 39-50.

Alley, R.B., Meese, D.A., Shuman, C.A., Gow, A.J., Taylor, K.C., Grootes, P.M., White, J.W.C., Ram, M., Waddington, E.D., Mayewski, P. and Zielinski, G.A. 1993. Abrupt increase in Greenland snow accumulation at the end of the Younger Dryas event. *Nature*, 362, 527-529.

Allison, J., Godwin, H. and Warren, S.H. 1952. Late-Glacial Deposits at Nazeing in the Lea Valley, North London. *Philosophical Transactions of the Royal Society of London*, B236, 169-240.

Andrews, J.T. 1983. Short ice age 230,000 years ago. *Nature*, 303, 21-22.

Andrews, P. 1990. *Owls, Caves and Fossils.* British Museum (Natural History), London.

Andrieu, V., Field, M.H., Ponel, P., Guiot, J., Guenet, P., de Beaulieu, J.-L., Reille, M. and Morzadec-Kerfourn, M.-T. 1997. Middle Pleistocene temperate deposits at Dingé, Ille-et-Vilaine, northwest France: pollen, plant and insect macrofossil analysis. *Journal of Quaternary Science*, 12 (4), 309-331.

Armstrong, A.L. 1929. Excavations at Creswell Crags, the Pin Hole Cave. *Transactions of the Hunter Archaeological Society,* 3, 116-122.

Arnold, E.N. and Burton, J.A. 1978. *A Field Guide to the Reptiles and Amphibians of Britain and Europe.* Collins, London.

Arnold, H.R. 1973 (ed.). *Provisional Atlas of the Amphibians and Reptiles of the British Isles.* Biological Records Centre, Monks Wood Experimental Station, Huntingdon.

Arnold, H.R. 1995. *Atlas of amphibians and reptiles in Britain.* Institute of Terrestrial Ecology

research publication no. 10, HMSO, London.

Arntzen, J.W. and Borkin, L. 1997. *Triturus* superspecies *cristatus* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 76-77.

Arntzen, J.W. and De Wijer, P. 1989. On the Distribution of the Palaearctic Newts (Genus *Triturus*) including the Description of a Five Species Pond in Western France. *British Herpetological Society Bulletin*, 30, 6-11.

Ashton, N.M, Bowen, D.Q., Holman, J.A., Hunt, C.O., Irving, B.G., Kemp, R.A., Lewis, S.G., McNabb, J., Parfitt, S. and Seddon, M.B. 1994. Excavations at the Lower Palaeolithic site at East Farm, Barnham, Suffolk 1989-92. *Journal of the Geological Society of London,* 151, 599-605.

Atkinson, T.C., Briffa, K.R. and Coope, G.R. 1987. Seasonal temperatures in Britain during the past 22 000 years, reconstructed using beetle remains. *Nature*, 325, 587-592.

Banks, B. 1989. Alpine newts in north east England. *British Herpetological Society Bulletin*, 30, 4-5.

Banks, B. 1997. Cumbria - Stronghold of the British Natterjack. *British Wildlife*, 9 (1), 1-6.

Barton, R.N.E. 1993. An interim report on the survey and excavations in the Wye Valley, 1993. *Proceedings of the University of Bristol Spelaeological Society*, 19 (3), 337-346.

Barton, R.N.E. 1994. Second interim report on the survey and excavations in the Wye Valley, 1994. *Proceedings of the University of Bristol Spelaeological Society*, 20, 63-73.

Barton, R.N.E., Price, C. and Proctor, C. 1997. Wye Valley Caves Project: Recent Investigations at King Arthur's Cave and Madawg Rockshelter. In: Lewis, S.G. and Maddy, D. (eds.) *The Quaternary of the South Midlands and the Welsh Marches: Field Guide.* Quaternary Research Association, London.

Bassinot, F.C., Labeyrie, L.D., Vincent, E., Quidelleur, X., Shackleton, N.J. and Lancelot, Y. 1994. The astronomical theory of climate and the age of the Brunhes-Matuyama magnetic reversal. *Earth and Planetary Science Letters*, 126, 91-108.

Beebee, T.J.C. 1974. The natterjack toad (*B. calamita*) in the British Isles; a study of past and present status. *British Journal of Herpetol*ogy, 5, 515-521.

Beebee, T.J.C. 1977. Environmental change as a cause of natterjack toad (*Bufo calamita*) declines in Britain. *Biological Conservation*, 11, 87-102.

Beebee, T.J.C. 1978. An attempt to explain the distributions of the rare herptiles *Bufo calamita, Lacerta agilis* and *Coronella austriaca* in Britain. *British Journal of Herpetology*, 5, 763-770.

Beebee, T.J.C. 1979. A review of scientific information pertaining to the natterjack toad *Bufo calamita* throughout its geographical range. *Biological Conserv*ation, 16, 107-134.

Beebee, T.J.C. 1981. Historical Aspects of British Herpetofauna Distribution: a reply. *British Journal of Herpetology*, 6, 178.

Beebee, T.J.C. 1983. *The Natterjack Toad.* Oxford University Press, Oxford.

Beebee, T.J.C. 1984. Possible origins of Irish natterjack toads (*Bufo calamita*). *British Journal of Herpetology*, 6, 398-402.

Beebee, T.J.C. 1985. Geographical variations in breeding activity patterns of the natterjack toad *Bufo calamita* in Britain. *Journal of Zoology, London*, 205, 1-8.

Beebee, T.J.C. 1995. Ever-earlier breeding migrations by alpine newts (*Triturus alpestris*) living wild in Britain. *British Herpetological Society Bulletin*, 51, 5-6.

Beebee, T.J.C. 1996. Pool our knowledge. Letter to *BBC Wildlife*, 14 (3), 97.

Beebee, T.J.C. 1997a. *Bufo calamita* Laurenti, 1768. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 120-121.

Beebee, T.J.C. 1997b. *Extraction and analysis of DNA from sub-fossil frog bones.* Report for English Nature, Peterborough.

Beebee, T.J.C. and Beebee, M.L. 1977. A quantitative study of metamorphosis in the natterjack toad, *Bufo calamita. British Journal of Herpetology*, 5, 689-693.

Beebee, T.J.C. and Griffin, J.R. 1977. A preliminary investigation into natterjack toad (*Bufo calamita*) breeding site characteristics in Britain. *Journal of Zoology, London*, 181, 341-350.

Bell, T. 1839. *A History of British Reptiles.* John Van Voorst, London.

Bell, T. 1859. The edible frog long a native of Foulmire Fen. *Zoologist*, 17, 6565.

Bender, M., Sowers, T., Dickson, M-L., Orchardo, J., Grootes, P., Mayewski, P.A. and Meese, D.A.. 1994. Climate correlations between Greenland and Antractica during the past 100,000 years. *Nature*, 372, 663-666.

Berger, A.L. 1978. Long-term variations of caloric insolation resulting from the earth's orbital elements. *Quaternary Research*, 9, 133-145.

Berglund, B.E., Bergsten, H., Björck, S., Kolstrup, E., Lemdahl, G. and Nordberg, K. 1994. Late Weichselian environmental change in southern Sweden and Denmark. *Journal of Quaternary Science*, 9 (2), 127-132.

Bishop, M.J. 1982. The mammal fauna of the early middle Pleistocene cavern infill site of Westbury-sub-Mendip, Somerset. *Palaeontological Association Special Paper*, 28, 1-108.

Björck, S. and Möller, P. 1987. Late Weichselian Environmental History in Southeastern Sweden during the Deglaciation of the Scandinavian Ice Sheet. *Quaternary Research*, 28, 1-37.

Björck, S., Kromer, B., Johnsen, S., Bennike, O., Hammarlund, D., Lemdahl, G., Possnert, G., Rassmussen, T.L., Wohlfarth, B., Hammer, C.U. and Spurk, M. 1996. Synchronized Terrestrial-Atmospheric Deglacial Records Around the North Atlantic. *Science*, 274, 1155-1160.

Björck, S., Rundgren, M., Ingólfsson, Ó. and Funder, S. 1997. The Preboreal oscillation around the Nordic Seas: terrestrial and lacustrine responses. *Journal of Quaternary Science*, 12 (6), 455-465.

Böhme, G. 1977. Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. *Wissenschaftliche Zeitxchrift Der Humboldt-Universitat Zu Berlin, Mathematik-Naturwissenschaft,* 26, 283-300.

Böhme, G. 1982a. Osteologische Anomalien bei anuren Amphibien (Salientia). *Wissenschafliche Zeitschrift der Humboldt-Universität zu Berlin, Math.-Nat. R.*, 31 (3), 201-207.

Böhme, G. 1982b. Biometrische Untersuchungen an Skelettelementen von Anuren. *Wissenschafliche Zeitschrift der Humboldt-Universität zu Berlin, Math.-Nat. R.*, 31 (3), 209-216.

Böhme, G. and Günther, R. 1979. Osteological studies in the European water frogs *Rana ridibunda, Rana lessonae* and *Rana "esculenta"* (Anura, Ranidae). *Mitt. Zool. Mus. Berlin*, 55 (1), 203-215.

Böhme, W. 1997. *Lacerta vivipara* Jacquin, 1787. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 268-269.

Bojanus, L.H. 1819-1821. *Anatome Testudinis Europaeae.* Vilnae et Lipsiae.

Bolkay, St. J. 1919. Osnove uporedne osteologije anurskich batrahija sa dodatkom o porijeklu Anura i sa sicom naravnoga sistema istih. *Glasnik Zemalj. Museja Bosni i Hercegovini, Sarajevo*, 1933, 31 (4), 277-358.

Bolkay, St. J. 1933. *Atlas to work Dr. St. Bolkay: Elements of the comparative osteology of the tailless batrachians.* Drzavna Stamparija, Sarajevo.

Bons, J. and Geniez, P. 1996. *Anfibios y Reptiles de Marruecos (Incluido Sáhara Occidental). Atlas Biogeográfico.* Asociación Herpetológica Española, Barcelona.

Boomsma, J.J. and Arntzen, J.W. 1985. Abundance, growth and feeding of natterjack toads (*Bufo calamita*) in a 4-year-old artificial habitat. *Journal of Applied Ecology*, 22, 395-405.

Borkin, L.J. and Veith, M. 1997. *Bufo bufo* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 118-119.

Böttcher, R. 1994. Niedere Wirdeltiere (Fische, Amphibien, Reptilien) aus dem Quartär von Stuttgart. *Stuttgarter Beitr. Natursk. Ser. B*, 215, 1-75.

Boulenger, G.A. 1884. On the origin of the edible frog in England. *Zoologist* (Series 3), 8, 265-269.

Boulenger, G.A. 1897-8. *The Tailless Batrachians of Europe.* Ray Society, London. (2 Volumes)

Boulenger, G.A. 1913. *The Snakes of Europe.* Methuen and Co. Ltd., London.

Bourne, A.G. 1884. On Certain Abnormalities in the Common Frog (*Rana temporaria*). *Quarterly Journal of Microscopic Science,* 24, 83-88.

Bowen, D.Q., Hughers, S., Sykes, G.A. and Miller, G.H. 1989. Land-sea correlations in the Pleistocene based on isoleucine epimerization in non-marine molluscs. *Nature*, 340, 49-51.

Bowen, D.Q. 1992. Aminostratigraphy of non-marine Pleistocene mollusca in Southern Britain. *Sveriges Geologiska Undersökning*, 81, 65-67.

Braithwaite, A.C., Buckley, J., Corbett, K.F., Edgar, P.W., Haslewood, E.S., Haslewood, G.A.D., Langton, T.E.S. and Whitaker, W.J. 1989. The Distribution in England of the Smooth Snake (*Coronella austriaca* Laurenti). *Herpetological Journal*, 1, 370-376.

Bramwell, D. 1960. Some Research into Bird Distribution in Britain During the Late Glacial and Post-Glacial Periods. *Bird Report of the Merseyside Naturalists Association*, 1959-60, 51-58.

Bramwell, D., Cartledge, K.M., Gilbertson, D.D., Griffin, C.M., Hunt, C.O., Jenkinson, R.D.S. and Samson, C. 1984. Steetley Quarry Cave: A 'Lost' Interglacial Site and Steetley Cave: A 5000 year old Badger Den. In: Jenkinson, R.D.S. and Gilbertson, D.D. (eds.). *In the Shadow of Extintion: A Quaternary Archaeology and Palaeoecology of the Lake, Fissures and Smaller Caves at Creswell Crags SSSI.* University of Sheffield, Sheffield, 75-87.

Bridgland, D.R. 1988. The Pleistocene fluvial stratigraphy and palaeogeography of Essex. *Proceedings of the Geologists' Association*, 99 (4), 291-314.

Bridgland, D.R. 1994 (ed.). *Quaternary of the Thames.* Chapman & Hall, London.

Bridgland, D.R., Allen, P.M., Currant, A.C., Gibbard, P.L., Lister, A.M., Preece, R.C., Robinson, J.E., Stuart, A.J. and Sutcliffe, A.J. 1988. Report of the Geologists' Association Field Meeting in north-east Essex, May 22nd-24th, 1987. *Proceedings of the Geologists' Association.* 99 (4), 315-333.

Bridgland, D.R., Gibbard, P.L. and Preece, R.C. 1990. The geology and significance of the interglacial sediments at Little Oakley, Essex. *Philosophical Transactions of the Royal Society of London*, B328, 307-339.

Briggs, D.J., Coope, G.R. and Gilbertson, D.D. 1985. *The chronology and environmental framework of early man in the Upper Thames Valley*. British Archaeological Reports, British Series 137, Oxford.

Briggs, D.J., Gilbertson, D.D., Griffin, C.M., Jenkinson, R.D.S., Stebbings, R.E. and Watts, C.M. 1984. Death, Disarticulation and Decay in an Eight Thousand Year Old Rock Fall In. Jenkinson, R.D.S. and Gilbertson, D.D. (eds.). *In the Shadow of Extintion: A Quaternary Archaeology and Palaeoecology of the Lake, Fissures and Smaller Caves at Creswell Crags SSSI* Unversity of Sheffield, Sheffield, 55-74.

Bringsøe, H. and Mikkelsen, U.S. 1993. The distribution of *Triturus alpestris* (Amphibia. Caudata) at its northern limit, in southern Denmark. *British Herpetological Society Bulletin*, 44. 16 28.

Buckingham, C.M., Roe, D.A. and Scott, K. 1996. A preliminary report on the Stanton Harcourt Channel Deposits (Oxfordshire, England): geological context, vertebrate remains and palaeolithic stone artefacts. *Journal of Quaternary Science*, 11 (5), 397-415.

Buckley, J. 1986. Water frogs in Norfolk. *Transactions of the Norfolk and Norwich Natural History Society*, 27 (3), 199-211.

Buckley, J. and Snell, C. 1995. *Species Action Plan: the pool frog Rana lessonae.* Report for English Nature, Peterborough.

Bury, H. 1950. Blashenwell tufa. *Proceedings of the Bournemouth Natural History Society*, 39, 48-51.

Busack, S.D. 1986. Biogeographic Analysis of the Herpetofauna Separated by the Formation of the Strait of Gibraltar. *National Geographic Research*, 2 (1), 7-36.

Cabela, A. 1997. *Anguis fragilis* Linnaeus, 1758. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 196-197.

Callander, J.G., Cree, J.E. and Ritchie, J. 1927. Preliminary Report on Caves Containing Palaeolithic Relics, Near Inchnadamph, Sutherland. *Proceedings of the Society of Antiquaries of Scotland,* 61, 169-172.

Campbell, J.B. 1969. Excavations at Creswell Crags. *Derbyshire Archaeological Journal*, 89, 47-58.

Campbell, J.B. 1977. Cathole, 1968: Later Upper Palaeolithic Mammals and Small Mammal Faunal Analysis. In: *The Upper Palaeolithic of Britain: A Study of Man and Nature in the Late Ice Age.* Clarendon Press, Oxford, 120-121.

Campbell, S. and Bowen, D.Q. 1989. *Geological Conservation Review: Quaternary of Wales.* Nature Conservancy Council, Peterborough.

Capula, M. 1990. *The Macdonald Encyclopedia of Amphibians and Reptiles.* Macdonald and Co. (Publishers) Ltd., London.

Carreck, J.N. 1957. A Late Pleistocene Rodent and Amphibian Fauna from Levaton, near Newton Abbot, South Devon. *Proceedings of the Geologists' Association*, 68, 304-308.

Chantell, C.J. 1964. Some Mio-Pliocene Hylids From the Valentine Formation of Nebraska. *American Midland Naturalist*, 72, 211-225.

Coborn, J. 1994. *The Mini-Atlas of Snakes of the World.* T.F.H. Publications, Inc., Neptune.

Collcutt, S.N. 1975. *The Stratigraphy of Creswell Crags.* MA Thesis, Department of Archaeology, University of Edinburgh.

Collcutt, S.N. 1984. The sediments. In: Green, H.S. (ed.) *Pontnewydd Cave. A Lower Palaeolithic hominid site in Wales.* National Museum of Wales, Cardiff, 31-77.

Coope, G.R. 1977. Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philosophical Transactions of the Royal Society of London*, B280, 313-340.

Coope, G.R. 1986. The Middle Devensian. In: Bowen, D.Q. and Harkness, D.D. (eds.). *NERC Radiocarbon Dating: 1975-1985. A review of the contribution to Quaternary Research by the NERC Radiocarbon Dating Laboratory over the last decade.* Natural Environment Research Council, London, 10-11.

Coope, G.R. and Lemdahl, G. 1995. Regional differences in the Lateglacial climate of northern Europe based on coleopteran analysis. *Journal of Quaternary Science*, 10 (4), 391-395.

Coope, G.R., Shotton, F.W. and Strachan, I. 1961. A Late Pleistocene Fauna and Flora from Upton Warren, Worcestershire. *Philosophical Transactions of the Royal Society of London*, B244, 379-421.

Corbet, K. 1989. *Conservation of European Reptiles and Amphibians*. Christopher Helm, London.

Coxon, P. and Waldren, S. 1995. The floristic record of Ireland's Pleistocene temperate stages. In: Preece, R.C. (ed.) *Island Britain: a Quaternary perspective*, Geological Society Special Publication 96, London, 243-267.

Coxon, P, Hall, A.R., Lister, A. amd Stuart, A.J. 1980. New evidence on the vertebrate fauna, stratigraphy and palaeobotany of the interglacial deposits at Swanton Morley, Norfolk. *Geol. Mag.*, 117 (6), 525-546.

Currant, A.P. 1984. The mammalian remains. In: Green, H.S. (ed.) *Pontnewydd Cave. A Lower Palaeolithic hominid site in Wales.* National Museum of Wales, Cardiff, 171-180.

Currant, A.P. 1987. Late Pleistocene Saiga Antelope *Saiga tatarica* on Mendip. *Proceedings of the University of Bristol Spelaeological Society*, 18 (1), 74-80.

Currant, A.P. 1989. The Quaternary origins of the modern British mammal fauna. *Biological Journal of the Linnean Society*, 38, 23-30.

Currant, A.P. 1996. Tornewton Cave and the Palaeontological Succession. In: Charman, D.J., Newnham, R.M. and Croot, D.G. (eds.) *The Quaternary of Devon and East Cornwall: Field Guide*. Quaternary Research Association, London, 174-180.

Currant, A.P. and Jacobi, R. 1997. Vertebrate faunas of the British Late Pleistocene and the chronology of human settlement. *Quaternary Newsletter*, 82, 1-8.

Dansgaard, W., White, J.W.C. and Johnsen, S.J. 1989. The abrupt termination of the Younger Dryas climate event. *Nature*, 339, 532-534.

Davies, M. 1989. Recent advances in cave archaeology in South-West Wales. In: Ford, T.D. (ed.) *Limestones and Caves of Wales*. Cambridge University Press, Cambridge, 79-91.

Davis, S. and Payne, S. 1992. 101 ways to deal with a dead hedgehog: notes on the preparation of

disarticulated skeletons for zoo-archaeological use. *Circaea*, 8(2), 95-104.

Dawkins, W.B. 1863. On a Hyaena-den at Wookey Hole, near Wells. No. II. *Quarterly Journal of the Geological Society of London*, 19 (1), 260-274.

Dawkins, W.B. 1876. On the mammalia and traces of Man in Robin Hood's Cave. *Quarterly Journal of the Geological Society of London*, 32, 240-259.

Dawkins, W.B. 1877. One the Mammal-Fauna of the Caves of Creswell Crags. *Quarterly Journal of the Geological Society of London*, 33, 589-612.

Degerbøl, M. and Krog, H. 1951. Den europaeiske Sumpskildpadde (*Emys orbicularis* L.) i Danmark. *Danmarks Geologiske Undersøgelse II. Raekke*, 78, 1-130.

Delcourt, H.R. and Delcourt, P.A. 1991. *Quaternary Ecology: a palaeoecological perspective* Chapman and Hall, London.

Devoy, R.J.N. (1995). Deglaciation, Earth crustal behaviour and sea-level changes in the determination of insularity: a perspective from Ireland. In Preece, R.C. (ed.) *Island Britain: a Quaternary perspectice*, Geological Society Special Publication No. 96, London, 181-208.

Dixon, S.B. 1998. *Molluscan signatures in the British Ipswichian.* Unpublished PhD thesis, Royal Holloway, University of London.

Duellman, W.E. and Trueb, L. 1986. *Biology of Amphibians.* John Hopkins Press Ltd., London.

Ecker, A. 1889. *The Anatomy of the Frog.* Clarendon Press, Oxford. (Translated by G. Haslam).

Estes, R. 1981. *Handbüch der Paläoherpetologie. Part 2: Gymphiona, Caudata.* Gustav Fischer Verlag, Stuttgart.

Estes, R. 1983. *Handbüch der Paläoherpetologie. Part 10A: Sauria terrestria, Amphisbaenia.* Gustav Fischer Verlag, Stuttgart.

Evans, J.G., French, C. and Leighton, D. 1978. Nabitat change in two late-glacial and post-glacial sites in southern Britain: the molluscan evidence. In: Limbrey, S. and Evans, J.G. (eds.) *The effect of man on the landscape: the lowland zone.* Council for British Archaeology Research Report, 21, 63-75.

Fairbanks, R.G. 1989. A 17,000-year glacio-eustatic sea level record: influence of glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*, 342, 637-642.

Fitter, R.S.R. 1959. *The Ark in Our Midst.* Collins, London.

Forbes, C.L., Joysey, K.A. and West, R.G. 1958. Post-glacial pelicans in Britain. *Geological Magazine*, 95, 53-160.

Ford, T.D. 1959. The Sutherland Caves. *Transactions of the British Cave Research Association,* 5, 141-187.

Forselius, S. 1962. Distribution and reproductive behaviour of *Rana esculenta* L. in the coastal area of N. Uppland, C. Sweden. *Zool. Bidrag. Uppsala*, 35, 517-528.

Francis, E.T.B. 1934. *The Anatomy of the Salamander.* Clarendon Press, Oxford.

Frazer, D. 1983. *Reptiles and Amphibians in Britain.* Bloomsbury Books, London.

French, C.A.I. 1994. *Excavation of the Deeping St. Nicholas Barrow Complex, South Lincolnshire.* Lincolnshire Archaeology and Heritage Report Series No. 1, Heritage Lincolnshire, Sleaford.

Frost, D.R. 1985. *Amphibian Species of the World. A Taxonomic and Geographical Reference.* Allen Press and The Association of Systematics Collections, Lawrence, Kansas.

Gadow, H. 1904. Reptilia and Amphibia of Cambridgeshire. In: Marr, J.E. and Shipley, A.E. (eds.). *Handbook to the Natural History of Cambridgeshire.* Cambridge University Press, Cambridge.

García París, M. 1997. *Hyla meridionalis* Boettger, 1874. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 126-127.

Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen, D., Grossenbacher, K., Haffner, P., Lescure, J., Martens, H., Martínez Rica, J.P., Maurin, H., Oliviera, M.E., Sofianidou, T.S., Veith, M. and Zuiderwijk, A. (eds.). 1997. *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris.

Gaupp, E. 1894. Das Hyo-Branchia-Skelet der Anuren und seine Umwandlung. *Morpholog. Arbeiten hrsg v. G. Schwalbe,* 3, 399-437.

Gaupp, E. 1896. *A. Ecker's und R. Wiedersheim's Anatomie des Frosches.* Friedrich Vieweg und Sohn, Braunschweig.

Gibbard, P.L. and Peglar, S.M. 1990. Palynology of the interglacial deposits at Little Oakley, Essex, and their correlation. *Philosophical Transactions of the Royal Society of London*, B328, 341-357.

Gibbard, P.L., Aalto, M.M., Coope, G.R., Currant, A.P., McGlade, J.M., Peglar, S.M., Preece, R.C., Turner, C., Whiteman, C.A. and Wrayton, R.C. 1996. Early Middle Pleistocene fossiliferous sediments in the Kesgrave Formation at Broomfield, Essex, England. In: Turner, C. (ed.). *The Early Middle Pleistocene in Europe.* A.A. Balkema, Rotterdam, 83-119.

Gislén, T. and Kauri, H. 1959. Zoogeography of the Swedish amphibians and reptiles with notes on their growth and ecology. *Acta Vertebratica*, 1 (3), 197-397.

Gleed-Owen, C.P. 1992. *The Flandrian Palaeoenvironmental History of Smoo Cave, Sutherland: Faunal and Sedimentological Evidence.* BSc Dissertation, Coventry Polytechnic.

Gleed-Owen, C.P. 1994. The Stomach Contents of a Grass Snake, *Natrix natrix*, Identified from Skeletal Remains. *British Herpetological Society Bulletin*, 50, 34-36.

Gleed-Owen, C.P. 1996. Amphibian Remains Identified from the Gut of a Grass Snake and a Polecat.. *British Herpetological Society Bulletin*, 57, 21-23.

Gleed-Owen, C. 1997a. The Devensian Lateglacial arrival of natterjack toad, *Bufo calamita*, in Britain and its implications for colonisation routes and land-bridges. *Quaternary Newsletter*, 81, 18 24.

Gleed-Owen, C.P. 1997b. Investigations of microvertebrate remains in South Wales caves. *Quaternary Newsletter*, 81, 57-58.

Gleed-Owen, C.P. 1997c. *On the Identification of green frog ilia, with reference to the zooarchaeological material from the fenland management project.* Supplementary report for English Nature, Peterborough.

Gleed-Owen, C.P. 1997d. The Origin of the West Coast Natterjacks - Kerry Across to Mersey? *British Herpetological Society Bulletin*, 60, 2-4.

Gleed-Owen, C.P. 1997e. *Subfossil herpetofaunal assemblages from ten Fenland sites, including evidence for the former presence of the pool frog* (Rana lessonae) *in Lincolnshire.* Unpublished report for English Nature, Peterborough.

Gleed-Owen, C.P. 1997f. The prehistory of the slow-worm in Britain. In: Riddell, A. (ed.) *The Slow-worm.* Kent Reptile and Amphibian Group & British Herpetological Society, Canterbury, 8-12.

Gleed-Owen, C.P. 1998. Amphibian remains from Cassington. *Journal of Quaternary Science,* 13 (2), in press.

Gleed-Owen, C.P. (submitted). The palaeoclimatic and biostratigraphic significance of herpetofaunal remains from the British Quaternary. In: Banham, P. (ed.). *Geological Society Special Publication.*

Gleed-Owen, C.P. and Joslin, P. 1996. *Zooarchaeological/ sub-fossil studies: the establishment and study of a reference collection of bone material* plus *analysis of sediment core samples from sites in Norfolk and Cambridgeshire.* Unpublished report for English Nature, Peterborough.

Gollman, G., Piálek, J., Szymura, J.M. and Arntzen, J.W. 1997a. *Bombina bombina* (Linnaeus, 1761). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 96-97.

Gollman, G., Szymura, J.M., Arntzen, J.W. and Piálek, J. 1997b. *Bombina variegata* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 98-99.

González, J.E. and Sanchiz, B. 1986. Consideraciones metodologicas sobre el analisis evolutivo: el caso de los morfotipos vertebrales actuales y fosiles del genero *Triturus* (Caudata, Salamandridae). *Estudios geologicos*, 42, 479-486.

Green, C.P., Coope, G.R., Currant, A.P., Holyoak, D.T., Ivanovich, M., Jones, R.L., Keen, D.H., McGregor, D.F.M. and Robinson, J.E. 1984. Evidence of two temperate episodes in the late Pleistocene deposits at Marsworth. *Nature*, 309, 778-781.

Green, H.S. 1984. *Pontnewydd Cave. A Lower Palaeolithic Hominid site in Wales.* National Museum of Wales, Cardiff.

Green, S. and Walker, E. 1991. *Ice Age Hunters. Neanderthals and Early Modern Hunters in Wales.* National Museum of Wales, Cardiff.

Green, H.S., Bull, P.A., Campbell, E., Coles, G. and Currant, A. 1986. Excavations at Little Hoyle (Longbury Bank), Wales in 1984. In: Roe, D.A. (ed.) *Studies in the Upper Palaeolithic of Britain and North-West Europe.* British Archaeological Reports, International Series 296, Oxford, 99-119.

Griffith, H. 1987. Spadefoot toads in South Wales: a prvisional report. *British Herpetological Society Bulletin*, 20, 29-30.

Grootes, P.M., Stuiver, M., White, J.W.C., Johnsen, S. and Jouzel, J. 1993. Comparison of oxygen isotope records from the GISP2 and GRIP Greenland ice cores. *Nature*, 366, 552-554.

Grossenbacher, K. 1997a. *Alytes obstetricans* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 94-95.

Grossenbacher, K. 1997b. *Rana temporaria* Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 158-159.

Grossenbacher, K. 1997c. *Rana dalmatina* Bonaparte, 1840. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 134-135.

Grüger, E. 1996. Palynostratigraphy of the Middle Pleistocene sequences from Göttingenm Ott-Strasse. In: Turner, C. (ed.). *The Early Middle Pleistocene in Europe.* A.A. Balkema, Rotterdam, 173-180.

Guillaume, Cl. P. 1997. *Podarcis muralis* (Laurenti, 768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 286-287.

Günther, R. 1997a. *Rana ridibunda* Pallas, 1771. In: Gasc *et al* (eds.) *Atlas of Amphibians and*

Reptiles in Europe. Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 154-155.

Günther, R. 1997b. *Rana lessonae* Camerano, 1882. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 148-149.

Günther, R. 1997c. *Rana esculenta* Linnaeus, 1758. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 138-139.

Gurney, D. 1993. Excavations and surveys in Norfolk 1992. *Norfolk Archaeology*, 41 (4), 522-532.

Guyétant, R. 1997. *Pelodytes punctatus* (Daudin, 1803). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 116-117.

Gwynn, A.M., Riley, F.T. and Stelfox, A.W. 1940. Report on a Further Exploration (1929) of the Caves of Keshcorran, Co. Sligo. *Proceedings of the Royal Irish Academy,* 46B, 81-95.

Hall, A.R. 1979. Pollen analysis of a peat sample associated with *E. orbicularis* from East Wretham, Norfolk. *Boreas*, 8, 371.

Hallock, L.A., Holman, J.A. and Warren, M.R. 1990. Herpetofauna of the Ipswichian Interglacial Bed (Late Pleistocene) of the Itteringham Gravel Pit, Norfolk, England. *Journal of Herpetology*, 24 (1), 33-39.

Hammarlund, D. and Keen, D.H. 1994. A Late Weichselian stable isotope and molluscan stratigraphy from southern Sweden. *GFF*, 116, 235-248.

Hecht, M.K. and LaDuke, T.C. 1988. Bolyerine vertebral variation: A problem for palaeoherpetology. *Acta Zoologica Cracoviensia*, 31 (24), 605-614.

Herre, W. 1949. Neue Tatsachen zur Stammesgeschichte der Schwanslurche. *Zool. Jahrb., Abt. Syst.*, 78, 217-236.

Herre, W. 1955. Die Fauna der miozänen Spaltenfüllung von Neudorf a. d. March (CSR.),

Amphibia (Urodela). *Ostear Akad Wissensch. Math.-Naturw. Abt. 1*, 164 (10), 783-803.

Hinton, M.A.C. 1952. Remains of Small Mammals. In: Allison, J., Godwin, H. and Warren, S.H. Late-Glacial Deposits at Nazeing in the Lea Valley, North London. *Philosophical Transactions of the Royal Society of London*, B236, 182-188.

Hodrová, M. 1981. Plio-Pleistocene frog fauna from Hajnácka and Ivonovce, Czechoslovakia. *Vestnik Ústredního ústavu geologického*, 56 (4), 215-224.

Hodrová, M. 1984. Salamandridae of the Upper Pliocene Ivanovce locality (Czechoslovakia). *Acta Universitatis Carolinae - Geologica*, 4, 331-352.

Hodrová, M. 1985. Amphibia of Pliocene and Pleistocene Vceláre localities (Slovakia). *Casopis pro mineralogii a geologii*, 30 (2), 145-161.

Holman, J.A. 1985. Herpetofauna of the Late Pleistocene Fissures Near Ightham, Kent. *Herpetological Journal*, 1, 26-32.

Holman, J.A. 1987a. Middle Pleistocene Herpetological Records from Interglacial Deposits at Sugworth, Near Oxford. *British Herpetological Society Bulletin,* 21, 5-7.

Holman, J.A. 1987b. Additional Records of British Pleistocene Amphibians and Reptiles. *British Hepretological Society Bulletin,* 19, 18-20.

Holman. J.A. 1987c. Herpetofauna of the Swanton Morley Site *(Pleistocene: Ipswichian)*, Norfolk. *Herpetological Journal*, 1, 199-201.

Holman, J.A., 1988. Herpetofauna of the Late Devensian/Early Flandrian Cow Cave Site, Chudleigh, Devon. *Herpetological Journal*, 1, 214-218.

Holman, J.A. 1989a. Additional Herpetological Records from the Middle Pleistocene (Cromerian Interglacial) Freshwater Bed, West Runton, Norfolk. *British Herpetological Society Bulletin*, 27, 9-12.

Holman, J.A. 1989b. Identification of *Bufo calamita* and *Bufo bufo* on the basis of skeletal elements. *British Herpetological Society Bulletin*, 29, 54-55.

Holman, J.A. 1990. New Records and Comments on British Pleistocene Cold-Stage Amphibians

and Reptiles. *British Herpetological Society Bulletin,* 34, 39-41.

Holman, J.A. 1991. Fossil History of the Grass Snake (Natrix natrix) (sic) With Emphasis on the British Fossil Record. *British Herpetological Society Bulletin*, 36, 8-13.

Holman, J.A. 1992a. The Boxgrove, England, Middle Pleistocene Herpetofauna: Palaeogeographic, Evolutionary, Stratigraphic and Palaeoecological Relationships. *Historical Biology,* 6, 263-279.

Holman, J.A. 1992b. *Hyla meridionalis* from the Late Pleistocene (Last Interglacial Age: Ipswichian) of Britain. *British Herpetological Society Bulletin,* 41, 12-14.

Holman, J.A. 1992c. Amphibians from a second century Roman well at Tiddington settlement, Warwickshire. *British Herpetological Society Bulletin*, 39, 5-7.

Holman, J.A. 1992d. Herpetofauna of Pleistocene (Ipswichian) Deposits at Selsey, West Sussex: The Earliest British Record of *Bufo calamita. Herpetological Journal,* 2, 94-98.

Holman, J.A. 1992e. Additional Records of *Natrix natrix* from the British Pleistocene, Including the First Record of a British Cold-Stage Snake. *British Herpetological Society Bulletin,* 40, 7-8.

Holman, J.A. 1993a. Pleistocene Herpetofauna of Westbury-Sub-Mendip Cave, England. *Cranium,* 10, 87-96.

Holman, J.A. 1993b. Herptiles from the Type Hoxnian (Middle Pleistocene Interglacial Stage) at Hoxne, Suffolk. *British Herpetological Society Bulletin,* 43, 33-35.

Holman, J.A. 1993c. British Quaternary Herpetofaunas: a History of Adaptations to Pleistocene Disruptions. *Herpetological Society,* 3, 1-7.

Holman, J.A. 1994. A new record of the aesculapian snake, *Elaphe longissima* (Laurenti), from the Pleistocene of Britain. *British Herpetological Society Bulletin*, 50, 37-39.

Holman, J.A. 1995a. *Rana temporaria*from a Late Pleistocene periglacial pit in Britain. *British Herpetological Society Bulletin*, 51, 27-29.

Holman, J.A. 1995b. Additional amphibians from a Pleistocene interglacial deposit at Purfleet, Essex. *British Herpetological Society Bulletin*, 52, 38-39.

Holman, J.A. 1995c. On the identification of Emydid (*Reptilia: Testudines*) shell bones in the Pleistocene of Britain. *British Herpetological Society Bulletin*, 53, 37-40.

Holman, J.A. and Clayden, J.D. 1988. Pleistocene Interglacial Herpetofauna of the Greenlands Pit, Purfleet, Essex. *British Herpetological Society Bulletin,* 26, 26-27.

Holman, J.A. and Clayden, J.D. 1990. A Late Pleistocene Interglacial Herpetofauna Near Shropham, Norfolk. *British Herpetological Society Bulletin*, 31, 31-35.

Holman, J.A. and Stuart, A.J. 1991. Amphibians of the Whitemoor Channel Early Flandrian Site near Bosley, East Cheshire; With Remarks on the Fossil Distribution of *Bufo calamita* in Britain. *Herpetological Journal,* 1, 568-573.

Holman, J.A., Clayden, J.D. and Stuart, A.J. 1988. Herpetofauna of the West Runton Freshwater Bed (Middle Pleistocene: Cromerian Interglacial), West Runton, Norfolk. *Bulletin of the Geological Society of Norfolk*, 38, 121-136.

Holman, J.A., Stuart, A.J. and Clayden, J.D. 1990. A Middle Pleistocene Herpetofauna from Cudmore Grove, Essex, England, and its Paleogeographic and Paleoclimatic Implications. *Journal of Vertebrate Palaeontology*, 10 (1), 86-94.

Ippen, R. and Heinrich, W-D. 1977. Pathologische Veranderungen an fossilen Extremitätenknochen von Anuren aus dem fossilen Tierbautensystem von Pisede bei Malchin. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Math.-Nat. R.*, 26, 301-305.

Irving, B. 1995. *Status of the pool frog* Rana lessonae *Camerano as a native British species based on zooarchaeological evidence from the English fens.* Technical Report 95/30, Environmental Archaeology Unit, University of York.

Isarin, R. 1997. *The climate in north-western Europe during the Younger Dryas. A comparison of multi-proxy climate reconstructions with simulation experiments.* Published Doctorate thesis, Vrije Universiteit, Amsterdam.

Isarin, R.F.B., Renssen, H. and Koster, E.A. 1997. Surface wind climate during the Younger Dryas in Europe as inferred from aeolian records and model simulations. *Palaeogeography, Palaeoclimatology, Palaeoecology,*

Isberg, O. 1929. Das ehemalige Vorkommen der Sumpfschildkröte (*Emys orbicularis* L.) in

Schweden und damit zusammenhängende klimatische Erscheinungen. *Arkiv für Zoologi.*, 21a (3), 1-52.

Ishchenko, V. 1997. *Rana arvalis* Nilsson, 1842. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 128-129.

Jacobi, R.M. 1986. A.M.S. Results from Cheddar Gorge - Trodden and Untrodden 'Lifeways'. In: Gowlett, J.A.J. and Hedges, R.E.M. (eds.) *Arhcaeological Results from Accelerator Dating.* Oxford University Commission for Archaeology Monograph Series, 11, 81-86.

Jacobi, R.M., Jacobi, E.B. and Burleigh, R. 1986. Kent's Cavern, Devon: Dating of the 'Black Band' and Human Settlement of the British Isles Following the Last Glacial Maximum. *Quaternary Newsletter*, 48, 10-12.

Jenkinson, R.D.S. 1984. *Creswell Crags: Late Pleistocene sites in the East Midlands.* British Archaeological Reports, British Series 122, Oxford.

Jenkinson, R.D.S. 1985. *Creswell Crags Visitor Centre Resource Collections: A User's Guide.* Creswell Crags Visitor Centre Occasional Report, 3.

Jenkinson, R.D.S. and Bramwell, D. 1984. The Birds of Britain: When Did they Arrive? In: Jenkinson, R.D.S. and Gilbertson, D.D. (eds.) *In the Shadow of Extintion: A Quaternary Archaeology and Palaeoecology of the Lake, Fissures and Smaller Caves at Creswell Crags SSSI.* University of Sheffield, Sheffield, 89-99.

Jenkinson, R.D.S. and Gilbertson, D.D. (eds.) 1984. *In the Shadow of Extintion: A Quaternary Archaeology and Palaeoecology of the Lake, Fissures and Smaller Caves at Creswell Crags SSSI.* University of Sheffield, Sheffield.

Jenkinson, R.D.S. and Gilbertson, D.D. 1984. The Legacy of Creswell. In: Jenkinson, R.D.S. and Gilbertson, D.D. (eds.) *In the Shadow of Extintion: A Quaternary Archaeology and Palaeoecology of the Lake, Fissures and Smaller Caves at Creswell Crags SSSI.* University of Sheffield, Sheffield, 1-11.

Jenkinson, R.D.S., Gilbertson, D.D., Griffin, C.M., Hunt, C.O., Rowe, P.J. and Coles, G. M. 1986. New Upper Palaeolithic Human Remains from Ronbin Hood's Cave, Creswell Crags SSSI, UK. In: Roe, D.A. (ed.) *Studies in the Upper Palaeolithic of Britain and Northwest Europe.*

British Archaeological Reports, International Series 296, Oxford, 89-97.

Johnsen, P. 1946. The Rock-pools of Bornholm and their fauna. *Vidensk. Medd. fra Dansk naturh. Foren.*, 109, 1-55.

Johnsen, S.J., Clausen, H.B., Dansgaard, W., Fuhrer, K., Gundestrup, N., Hammer, C.U., Iversen, P., Jouzel, J., Stauffer, B. and Steffensen, J.B. 1992. Irregular glacial interstadials recorded in a new Greenland ice core. *Nature*, 359, 311-313.

Johnson, R.H., Franks, J.W. and Pollard, J.E. 1970. Some Holocene faunal and floral remains in the Whitemoor Channel at Bosley, East Cheshire. *Staffordshire Journal of Field Studies*, 10, 65-74.

Jones, R.L. and Keen, D.H. 1993. *Pleistocene Environments in the British Isles*. Chapman and Hall, London.

Jouzel, J., Raisbeck, G., Benoist, J.P., Yiou, F., Lorius, C., Raynaud, D., Petit, J.R., Barkov, N.I., Korotkevitch, Y.S. and Kotlyakov, V.M. 1989. A Comparison of Deep Antarctic Ice Cores and Their Implications for Climate between 65,000 and 15,000 Years Ago. *Quaternary Research*, 31, 135-150.

Kabisch, K. 1997. *Natrix natrix* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe*. Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 370-371.

Keen, D.H. 1979. The Molluscan Fauna of a Flandrian Tufa at Lower Beck, Malham, North Yorkshire. *Journal of Conchology*, 33, 173-178.

Keen, D.H., Jones, R.L., Evans, R.A. and Robinson, J.E. 1988. Faunal and floral assemblages from Bingley Bog, West Yorkshire, and their significance for Late Devensian and early Flandrian environmental changes. *Proceedings of the Yorkshire Geological Society*, 47 (2), 125-138.

Keen, D.H., Van Vliet-Lanoë, B. and Lautridou, J-P. 1996. Two long sedimentary records from Jersey, Channel Islands: stratigraphic and pedological evidence for environmental change during the last 200 kyr. *Quaternaire*, 7 (1), 3-13.

Kerney, M.P. 1977. A Proposed Zonation Scheme for Late-glacial and Postglacial Deposits Using Land Mollusca. *Journal of Archaeological Science*, 4, 387-390.

Kerney, M.P. and Cameron, R.A.D. 1979. *A Field Guide to the Land Snails of Britain and North-West Europe.* Collins, London.

Kerney, M.P., Preece, R.C. and Turner, C. 1980. Molluscan and plant biostratigraphy of some late Devensian and Flandrian deposits in Kent. *Philosophical Transactions of the Royal Society of London*, B291, 1-43.

Kitagawa, H. and van der Plicht, J. 1998. Atmospheric Radiocarbon Calibration to 45,000 yr B.P.: Late Glacial Fluctuations and Cosmogenic Isotope Production. *Science*, 279, 1187-1190.

Korsós, Z. and Bischoff, W. 1997. *Lacerta agilis* Linnaeus, 1758. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 230-231.

Kuzmin, S.L. and Zuiderwijk, A. 1997. *Triturus vulgaris* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 88-89.

Lacaille, A.D. and Grimes, W.F. 1955. The prehistory of Caldey. *Archaeologia Cambrensis*, 104, 85-165.

Lamb, H.H. 1977. The late Quaternary history of the climate of the British Isles. In: Shotton, F.W. (ed.) *British Quaternary studies: recent advances.* Clarendon Press, Oxford, 283-298.

Lamb, H.H., Lewis, R.P.W. and Woodroffe, A. 1966. Atmospheric circulation and the main climatic variables between 8000 to 0 BC: meteorological evidence. In: Sawyer, J.S. (ed.) *Proceedings of the International Symposium on World Climate 8000 to 0 BC.* Royal Meteorological Society, London, 174-217.

Lambeck, K. 1995. Late Devensian and Holocene shorelines of the British Isles and North Sea from models of glacio-hydro-isostatic rebound. *Journal of the Geological Society*, 152, 437-448.

Lambeck, K. 1996. Glaciation and sea-level change for Ireland and the Irish Sea since Late Devensian/Midlandian time. *Journal of the Geological Society*, 153, 853-872.

Lane, T. 1993. *Early/Middle Saxon Settlement, Chopdike Drove, Gosberton, Lincolnshire.* Unpublished Assessment Report, Heritage Lincolnshire, Sleaford.

Langton, T.E.S. 1996. Native? I doubt it. Letter to *BBC Wildlife*, 14 (1), 88.

Lawson, T.J. 1981. The 1926-7 excavations of the Creag nan Uamh bone caves, near Inchnadamph, Sutherland. *Proceedings of the Society of Antiquaries of Scotland,* 111, 7-20.

Lawson, T.J. 1995. The Creag Nan Uamh Caves. in Lawson, T.J. (ed.). *The Quaternary of Assynt and Coigach: Field Guide.* Quaternary Research Association, Cambridge, 87-103.

Lawson, T.J. and Bonsall, C. 1986. Early Settlement in Scotland: The Evidence From Reindeer Cave, Assynt. *Quaternary Newsletter*, 49, 1-7.

Legge, A.J. 1995. A method for the preparation of very small animal skeletons. *Circaea*, 10 (2), 81.

Leighton, G.R. 1903. *The Life-History of British Lizards and Their Local Distribution in the British Isles.* Simpkin, Marshall and Co. Ltd., London.

Lister, A.M. 1992. Mammalian Fossils and Quaternary Biostratigraphy. *Quaternary Science Reviews*, 11, pp. 329-344.

Lister, A.M., McGlade, J.M. and Stuart, A.J. 1990. The Early Middle Pleistocene vertebrate fauna from Little Oakley, Essex. *Philosophical Transactions of the Royal Society of London*, B328, 359-385.

Lizana, M. 1997. *Pelobates cultripes* (Cuvier, 1829). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 108-109.

Lowe, J.J. and Gray, J.M. 1980. The Stratigraphic Subdivision of the Lateglacial of NW Europe: A Discussion. In: Lowe, J.J., Gray, J.M. and Robinson, J.E. (eds.) *Studies in the Lateglacial of North-West Europe.* Pergamon Press, Oxford, 157-175.

Lowe, J.J. and Walker, M.J.C. 1980. Problems Associated with Radiocarbon Dating the Close of the Lateglacial Period in the Rannoch Moor Area, Scotland. In: Lowe, J.J., Gray, J.M. and Robinson, J.E. (eds.) *Studies in the Lateglacial of North-West Europe.* Pergamon Press, Oxford, 123-137.

Lyman, R.L. 1994. *Vertebrate Taphonomy.* Cambridge University Press, Cambridge.

Macgregor, H.C., Sessions, S.K. and Arntzen, J.W. 1990. An integrative analysis of phylogenic relationships among newts of the genus *Triturus* (family Salamandridae), using comparative biochemistry, cytogenetics and reproductive interactions. *Journal of Evolutionary Biology*, 3, pp. 329-373.

Maddy, D., Lewis, S.G., Scaife, R.G., Bowen, D.Q., Coope, G.R., Green, C.P., Hardaker, T., Keen, D.H., Rees-Jones, J., Parfitt, S. and Scott, K. 1998. The Upper Pleistocene deposits at Cassington, near Oxford, UK. *Journal of Quaternary Science*, in press.

Madej, Z. 1965. Variations in the sacral region of the spine in *Bombina bombina* (Linnaeus, 1761) and *Bombina varegata* (Linnaeus, 1758) (Salientia, Discoglossidae). *Acta Biologica Cracoviensia Series: Zoologia*, 8, 185-197.

Mahoney, R. 1966. *Laboratory Techniques in Zoology*. Butterworths, London, 327-351.

Mangerud, J., Andersen, S.T., Berglund, B.E. and Donner, J.J. 1974. Quaternary stratigraphy of Norden, a proposal for terminology and classification. *Boreas*, 3, 109-127.

Markert, D. 1975. Schlüssel zur Bestimmung der Wirbel süddeutscher Ophidier und dessen Anwendung auf pleistozän/holozänes Reptilmaterial aus dem Euerwanger Bühl (Franken). *N. Jb. Geol. Paläont. Abh.*, 149 (2), 211-226.

Martínez Rica, J.P. 1997. Chapter 2: General features of European climate and vegetational consequences on the distribution of herpetofauna. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe*. Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 17-22.

Mattison, C. 1992. *Lizards of the world*. Blandford, London.

Maw, G. 1866. On the Occurrence of Extensive Deposits of Tufa in flintshire. *Geological Magazine*, 3, 253-256.

Mayer, W. and Bischoff, W. 1996. Beiträge zur taxonomischen Revision der Gattung *Lacerta* (Reptilia: Lacertidae). Teil 1: *Zootoca, Omanosaura, Timon* und *Teira* als eigenstandige Gattungen. *Salamandra*, 32 (3), 163-170.

McBurney, C.B.M. 1959. Report on the first season's fieldwork on British Upper Palaeolithic cave deposits. *Proceedings of the Prehistoric Society*, 25, 260-269.

Meijer, T. and Preece, R.C. 1996. Malacological evidence relating to the stratigraphical position of the Cromerian. In: Turner, C. (ed.) *The Early Middle Pleistocene in Europe*. A.A. Balkema, Rotterdam, 53-82.

Mello, J.M. 1875. On some bone caves in Creswell Crags. *Quarterly Journal of the Geological Society of London,* 31, 679-691.

Menzies, J.I. 1962. The marsh frog (*Rana esculenta ridibunda* Pallas) in England. *British Journal of Herpetology*, 43-54 and 89-90.

Merry, J.S. 1995. *The palaeoenvironment of interglacial deposits at Deeping St. James, Lincolnshire.* Unpublished BSc dissertation, Coventry University.

Mitchell, G.F. 1960. The Pleistocene History of the Irish Sea. *Advancement of Science*, 17, 313-325.

Mitchell, G.F., Penny, L.F., Shotton, F.W. and West, R.G. 1973. *A correlation of Quaternary deposits in the British Isles.* Geological Society of London Special Report Number 4, Geological Society of London.

Mlynarski, M. 1960. Pliocene Amphibians and Reptiles from Rebielice Królewskie (Poland). *Acta Zoologica Cracoviensia,* 5(4), 131-153.

Mlynarski, M. 1962. Notes on the Amphibian and Reptilian Fauna of the Polish Pliocene and Early Pleistocene. *Acta Zoologica Cracoviensia.*, 7 (2), 177-193.

Mlynarski, M. 1976. *Handbüch der Paläoherpetologie. Part 7: Testudines.* Gustav Fischer Verlag, Stuttgart.

Morrison, P. 1994. *Mammals, Reptiles and Amphibians of Britain and Europe.* Macmillan, London and Basingstoke.

Naulleau, G. 1997a. *Lacerta viridis* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 266-267.

Naulleau, G. 1997b. *Coluber viridiflavus* Lacepede, 1789. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National

d'Histoire Naturelle, Paris, 342-343.

Naulleau, G. 1997c. *Elaphe longissima* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 356-357.

Naulleau, G. and Schätti, B. 1997. *Natrix maura* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 368-369.

Naylor, B.G. 1978a. *The systematics of fossil and recent salamanders (Amphibia: Caudata), with special reference to the vertebral column and trunk musculature.* Unpublished PhD Thesis, University of Alberta, Edmonton.

Naylor, B.G. 1978. The frontosquamosal arch in newts as a defence against predators. *Canadian Journal of Zoology*, 56, 2211-2216.

Necas, P, Modry, D. and Zavadil, V. 1997. *Czech Recent and Fossil Amphibians and Reptiles: An Atlas and Field Guide.* Edition Chimaira, Frankfurt.

Nemec, J. 1945. Osteology of isolated anuran bones from Stranska Skala near Brno (Lower Quaternary). *Studia Musei Moraviae, Anthropos.*, 20 (N.S., 12), 21-33.

Newton, A. 1862. On the Discovery of Ancient Remains of *Emys lutaria* in Norfolk. *Annual Magazine of Natural History*, 10, 224-228.

Newton, E.T. 1879. Notes on some Fossil Remains of *Emys lutaria* from the Norfolk Coast. *Geological Magazine*, 6, 304-306.

Newton, E.T. 1882a. Notes on the Vertebrata of the Pre-Glacial Forest Bed Series of the East of England. *Geological Magazine*, 9, 7-9.

Newton, E.T. 1882b. *The Vertebrata of the Forest Bed series of Norfolk and Suffolk.* Memoirs of the Geol. Survey of the United Kingdom, HMSO, London.

Newton, E.T. 1884. Revised list of Vertebrata from the Forest-Bed Series. *Transactions of the Norfolk and Norwich Naturalists' Society*, 3 (5), 654-656.

Newton, E.T. 1891. *The Vertebrata of the Pliocene Deposits of Britain.* Memoirs of the Geological Society of the United Kingdom. HMSO, London.

Newton, E.T. 1894. The Vertebrate Fauna Collected by Mr. Lewis Abbott from the Fissure Near Ightham, Kent. *Quarterly Journal of the Geological Society,* 5, 188-211.

Newton, E.T. 1917. Notes on Bones Found in the Creag nan Uamh Cave, Inchnadamff, Assynt, Sutherland. *Proceedings of the Royal Society of Edinburgh,* 37, 327-349.

Nilson, G. and Andrén, C. 1997. *Vipera berus* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 388-389.

Nistri, A., Corti, C., Vanni, S. and Lanza, B. 1997. *Natrix tessellata* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 372-373.

Nöllert, A. 1997. *Pelobates fuscus* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 110-111.

Northcote, E.M. 1980. Some Cambridgeshire Neolithic to Bronze Age birds and their presence or absence in England in the Late Glacial and early Flandrian. *Journal of Archaeological Science,* 7, 379-380.

Ove, P. and Persson, E. 1980. Appendix 1: The osteological analysis of the cremated and unburned bone material at the megalithic cemetery at Carowmore, Co. Sligo, Ireland. In: Burenhult, G. *The Archaeological Excavation at Carrowmore, Co. Sligo, Ireland. Excavation Sessions 1977-1979.* G. Burenhult Forlag, Sweden, 117-128.

Ovenden, D., Corbet, G. and Arnold, N. 1979. *A handguide to the wild animals of Britain and Europe.* Diamond Books, London.

Ovey, C.D. 1964. (ed.) *The Swanscombe Skull. A survey of research on a Pleistocene site.* Royal Anthropological Institute of Great Britain and Ireland, Occasional Paper No. 20.

Owen, F.J. 1990. *The Potentialities of Amphibian Remains in Palaeoenvironmental Reconstruction.* Unpublished MSc Dissertation, University of Sheffield.

Özeti, N. 1967. The Morphology of the Salamander *Mertensiella luschani* (Steindachner) and the Relationships of *Mertensiella* and *Salamandra*. *Copeia*, 2, 287-298.

Parker, W.K. 1871. On the Structure and Development of the Skull of the Common Frog (*Rana temporaroa,* L.). *Philosophical Transactions of the Royal Society of London,* 161 (1), 137-208.

Parker, W.K. 1882. On the morphology of the skull in the Amphibia Urodela. *Transactions of the Linnéan Society London (2, Zool.)*, 2, 165-209.

Parker, W.N. 1897. *Elements of the Comparative Anatomy of Vertebrates. Adapted from the German of Dr. Robert Widersheim.* Macmillan and Co., London.

Peach, B.N. and Horne, J. 1917. The Bone-Cave in the Valley of Allt nan Uamh (Burn of the Caves), near Inchnadamff, Assynt, Sutherlandshire. *Proceedings of the Royal Society of Edinburgh,* 37, 327-349.

Peteet, D.M. 1992. The palynological expression and timing of the Younger Dryas event - Europe versus eastern North America. In: Bard, E. and Broecker, W.S. (eds.). *The Last Deglaciation: Absolute and Radiocarbon Chronologies.* NATO ASI Series, Vol. I 2, Springer-Verlag, Berlin and Heidelberg, 327-344.

Peters, G. 1977. Die Reptilien aus dem fossilen Tierbautensystem von Pisede bei Malchin. Part I: and Part I: Analyse des Fundgutes. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Math.-Nat.*, 26 (3), 307-320.

Pilling, J.A. 1953. Notes on Smoo Cave, Sutherland, Scotland. *Transactions of the British Cave Research Association*, 3(22), 277-284.

Pinto Llona, A.C. and Andrews, P. 1996. Amphibian Taphonomy from Cave Deposits in England. *Communicación de la II Reunión de Tafonomía y fosilización*, 1996, 327-330.

Pinto Llona, A.C. and Andrews, P. 1998. Amphibian taphonomy and its application to the fossil record of Dolina (middle Pleistocene, Atapuerca, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology*, in press.

Podloucky, R. 1997. *Emys orbicularis* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 170-171.

Pollard, T. 1992. *Smoo Cave.* Report by Glasgow University Archaeological Research Division.

Powell, T.G.E. and Daniel, G.E. 1956. *Barclodiad y Gawres. The excavation of a Megalithic chamber tomb in Anglesey.* Liverpool University Press, Liverpool.

Pratt, C.W.M. 1946. The Plane of Fracture of the Caudal Vertebrae of Certain Lacertilians. *Journal of Anatomy*, 80, 184-188.

Preece, R.C. 1979. The Molluscan Fauna of an Early Postglacial Tufa at Totland, Isle of Wight. *Journal of Conchology*, 30, 35-42.

Preece, R.C. 1980. The biostratigraphy and dating of the tufa deposit at the Mesolithic site at Blashenwell, Dorset, England. *Journal of Archaeological Science*, 7, 345-362.

Preece, R.C. 1990. The molluscan fauna of the Middle Pleistocene interglacial deposits at Little Oakley, Essex, and its environmental and stratigraphical implications. *Philosophical Transactions of the Royal Society of London*, B328, 387-407.

Preece, R.C. 1995. Mollusca from interglacial sites at three critical sites in the Lower Thames. In: Bridgland, D.R., Allen, P. and Haggart, B.A. (eds.) *The Quaternary of the Lower Reaches of the Thames.* Field Guide, Quaternary Research Association, Durham, 53-60.

Preece, R.C. and Robinson, J.E. 1982. Molluscan and Ostracod Faunas from Postglacial Tufaceous Deposits in County Offaly. *Proceedings of the Royal Irish Academy*, 82B, 115-131.

Prestwich, J. 1855. On a Fossiliferous Bed of the Drift Period near the Reculvers. *Quarterly Journal of the Geological Society of London*, 11, 110-112.

Proctor, C. 1996. Kent's Cavern. In: Charman, D.J., Newnham, R.M. and Croot, D.G. (eds.) *The Quaternary of Devon and East Cornwall: Field Guide.* Quaternary Research Association, London, 163-167.

Pumphrey, J.R. 1956. Contents of the hearth sample. In: Powell, T.G.E. and Daniel, G.E. *Barclodiad y Gawres. The excavation of a Megalithic chamber tomb in Anglesey.* Liverpool University Press, Liverpool, 16-17.

Pye, K., Stokes, S. and Neal, A. 1995. Optical dating of aeolian sediments from the Sefton coast, northwest England. *Proceedings of the Geologists' Association*, 106, 281-292.

Rabeder, G. 1977. Wirbeltierreste aus einer mittelpleistozänen Spaltenfüllung im Leithakalk von St. Margarethen im Burgenland. *Beitr. Paläont. Österr.*, 3, 79-103.

Rafinski, J. and Pecio, A. 1989. Craniometric Studies on the Species of the Genus *Triturus*, Rafinesque, 1815 (Amphibia, Salamandridae). *Folia Biologia (Kraków)*, 37 (3-4), 131-150.

Rage, J.-C. 1974. Les Batraciens des Gisements Quaternaires Europeens Determination Osteologique. *Bulletin de la Société Linnéenne de Lyon*, 43 (8), 276-289.

Rage, J.-C. 1984. *Handbüch der Paläoherpetologie. Part 11: Serpentes.* Gustav Fischer Verlag, Stuttgart.

Rage, J.-C. 1997. Chapter 3: Palaeobiological and palaeogeographical background of the European herpetofauna. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 23-28.

Rage, J.-C. and Ford, R.L.E. 1980. Amphibians and Squamates from the Upper Eocene of the Isles of Wight. *Tertiary Research*, 3 (2), 47-60.

Raxworthy, C.J., Kjølbye-Biddle, B. and Biddle, M. 1990. An archaeological study of frogs and toads from the eighth to sixteenth century at Repton, Derbyshire. *Herpetological Journal*, 1, 504-509.

Reid, C. 1882. The Geology of the country around Cromer. *Memoirs of the Geological Society of England and Wales.*

Reid, C. 1890. The Pliocene deposits of Britain. *Memoirs of the Geological Society of the United Kingdom.*

Ridewood, W.G. 1897. On the Structure and Development of the Hyobranchial Skeleton of the Parsley-Frog (*Pelodytes punctatus*). *Proceedings of the Zoological Society,* 1897, 577-595.

Roberts, A. (ed.). 1996. Evidence for Late Pleistocene and Early Holocene Human Activity and Environmental Change from the Torbryan Valley, South Devon. In: Charman, D.J., Newnham, R.M. and Croot, D.G. (eds.) *The Quaternary of Devon and East Cornwall: Field Guide.* Quaternary Research Association, London, 168-204.

Roberts, A. In prep. *The History of a Valley: Human Activity and Environmental Change in the*

Torbryan Valley, Devon. British Museum Press, London.

Roberts, M.B., Bates, M.R., Bergman, C., Currant, A.P., Haynes, J.R., Macphail, R., McConnell, A., Scaife, R., Unger-Hamilton, R. and Whatley, R.C. 1986. Excavations of the Lower Palaeolithic Site at Amey's Eartham Pit, Boxgrove, West Sussex: A Preliminary Report. *Proceedings of the Prehistoric Society*, 52, 215-245.

Rodwell, J.S. (ed.) 1991. *British Plant Communities Volume 1: Woodlands and Scrub.* Cambridge University Press, Cambridge.

Rolleston, G., Lane Fox, A., Busk, G., Dawkins, W.B., Evans, J. and Hilton-Price, F.G. 1878. Report of a committee ... appointed for the purpose of examining two caves containing human remains, in the neighbourhood of Tenby. *Report of the British Association for the Advancement of Science (Dublin)*, 48, 207-217.

Rollinat, R. 1946. *La Vie des Reptiles de la France Centrale.* Libraire Delagrave, Paris (3rd edition).

Romer, A.S. 1956. *Osteology of the Reptiles.* University of Chicago Press, Chicago.

Roth, P. 1997. *Bufo viridis* Laurenti, 1758. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 122-123.

Saint Girons, H. 1997. *Vipera aspis* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 386-387.

Sanchiz, F.B. 1977. La Familia Bufonidae (Amphibia, Anura) en el Terciario Europea. *Trabajos sobre Neogeno-Cuatanario*, 8, 75-111.

Sanchíz, B. 1988. On the presence of zygosphene-zygantrum vertebral articulations in salamandrids. *Acta Zoologica Cracoviensia*, 31 (16), 493-504.

Sanchiz, F.B. and Mlynarski, M. 1979. Remarks on the Fossil anurans from the Polish Neogene. *Acta Zoologica Cracoviensia*, 24 (3), 153-174.

Saunders, J.T., Manton, S.M. and Brown, M.E. 1969. *A Manual of Practical Vertebrate*

Morphology. Clarendon Press, Oxford (4th edition).

Savory, H.N. 1973. Excavations at the Hoyle, Tenby, in 1968. *Archaeologia Cambrensis*, 122, 18-34.

Scharff, R.F., Praeger, R.Ll., Coffey, G., Cole, G.A.J., Cunningham, D.J., Lamplugh, G.W., McHenry, A. and Ussher, R.J. 1902. The Exploration of Kesh Caves, County Sligo, Ireland. *Geological Magazine*, 9, 505-510.

Scholz, K.P. 1993. *Untersuchungen zur Phylogenie der Familie Salamandridae.* Unpublished Diplomarbeit, Philipps-Universität, Marburg.

Schreve, D.C. 1998. *Mammalian biostratigraphy of the later Middle Pleistocene in Britain.* Unpublished PhD thesis, University College, London.

Sejrup, H.P., Haflidason, H. and Kristensen, D.K. 1995. Last Interglacial and Holocene climatic development in the Norwegian Sea region: ocean front movements and ice core data. *Journal of Quaternary Science*, 10 (4), 385-390.

Shackleton, N.J. 1987, Oxygen Isotopes, Ice Volume and Sea Level. *Quaternary Science Reviews*, 6, 183-190.

Shackleton, N.J. and Opdyke, N.D. 1973. Oxygen Isotope and Palaeomagnetic Stratigraphy of Equatorial Pacific Core V28-238: Oxygen Isotope Temperature and Ice Volumes on a 10^5 and 10^6 Year Scale. *Quaternary Research*, 3, 39-55.

Shackleton, N.J. and Opdyke, N.D. 1976. Oxygen Isotope and Palaeomagnetic Stratigraphy of Pacific Core V28-239: Late Pliocene to Latest Pleistocene. *Geological Society of America Memoir*, 145, 449-464.

Shephard-Thorn, E.R. and Wymer, J.J. 1977. *South East England and the Thames Valley.* X INQUA Congress Excursion Guide, Geo Abstracts Ltd., UEA, Norwich.

Singer, R., Wymer, J., Gladfelter, B.G. and Wolff, R.G. 1973. Excavations of the Clactonian Industry at the Golf Course, Clacton-on-Sea, Essex. *Proceedings of the Prehistoric Society*, 39, 6-74.

Sjögren, P. 1991. Genetic variation in relation to demography of peripheral pool frog populations

(*Rana lessonae*). *Evolutionary Ecology*, 5, 248-271.

Smith, M. 1949. The Edible Frog and the Marsh Frog in England. *Zoo Life*, 4, 55-58.

Smith, M.A. 1969. *The British Amphibians and Reptiles.* Collins, London (4th edition).

Snell, C. 1994. The Pool Frog - a neglected native? *British Wildlife*, 6 (1), 1-4.

Snell, C. 1996. *Pool Frog Recovery Project (Part I: Survey, Part II: Management Recommendaions).* Report for English Nature, Peterborough.

Snelling, J.R. 1975. A Fossil Mollusc Fauna at Purfleet, Essex. *Essex Naturalist*, 33, 104-108.

Sprugel, D.G. 1991. Disturbance, Equilibrium, and Environmental Variability: What is 'Natural' Vegetation in a Changing Environment? *Biological Conservation*, 58, 1-18.

Street, D. 1979. *The Reptiles of Northern and Central Europe.* B.T. Batsford Ltd., London.

Strenski, E. 1995. *Analysis of Anuran Skeletal Remains from Kitley Caves, Yealmpton.* Unpublished MSc Dissertation, University of Sheffield.

Strijbosch, H. 1997. *Coronella austriaca* Laurenti, 1768. In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 344-345.

Stringer, C.B. 1984. The hominid finds. In: Green, H.S. (ed.) *Pontnewydd Cave. A Lower Palaeolithic hominid site in Wales.* National Museum of Wales, Cardiff, 159-177.

Stringer, C.B., Andrews, P. and Currant, A.P. 1996. Palaeoclimatic significance of mammalian faunas from Westbury Cave, Somerset, England. In: Turner, C. (ed.) *The Early Middle Pleistocene in Europe.* A.A. Balkema, Rotterdam, 133-143.

Stuart, A.J. 1974. Pleistocene History of the British Vertebrate Fauna. *Biological Review*, 49, 225 266.

Stuart, A.J. 1975. The vertebrate fauna of the type Cromerian. *Boreas*, 2, 63-76.

Stuart, A.J. 1976. The history of the mammal fauna during the Ipswichian/Last interglacial in

England. *Philosophical Transactions of the Royal Society of London*, B276, 221-250.

Stuart, A.J. 1979. Pleistocene occurrences of the European pond tortoise (*Emys orbicularis* L.) in Britain. *Boreas*, 8, 359-371.

Stuart, A.J. 1980. The vertebrate fauna from the interglacial deposits at Sugworth, near Oxford. *Philosophical Transactions of the Royal Society of London*, B289, 87-97.

Stuart, A.J. 1982. *Pleistocene vertebrates in the British Isles*. Longman, London and New York.

Stuart, A.J. 1996. Vertebrate faunas from the early Middle Pleistocene of East Anglia. In: Turner, C. (ed.) *The Early Middle Pleistocene in Europe*. A.A. Balkema, Rotterdam, 9-24.

Stuiver, M. and Reimer, P.J. 1993. Extended ^{14}C data base and revised CALIB 3.0 ^{14}C Age Calibration Program. *Radiocarbon*, 35, 215-230.

Stumpel, A. *Hyla arborea* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe*. Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 124-125.

Sutcliffe, A.J. 1995. Insularity of the British Isles 250 000-30 000 years ago: the mammalian, including human, evidence. In: Preece, R.C. (ed.) *Island Britain: a Quaternary perspective*, Geological Society Special Publication No. 96, London, 127-140.

Sutcliffe, A.J. and Zeuner, F.E. 1962. Excavations in the Torbryan Caves, Devonshire. I. Tornewton Cave. *Proceedings of the Devon Archaeological Exploration Society*, 5, 127-145.

Szyndlar, Z. 1984. Fossil Snakes from Poland. *Acta Zoologica Cracovensia*, 28(1), 3-156.

Szyndlar, Z. 1991. A Review of Neogene and Quaternary Snakes of Central and Eastern Europe. Part I: Scolecophidia, Boidae, Colubrinae. *Estudios geol.*, 47 103-126.

Taylor, R.H.R. 1948. The Distribution of Reptiles and Amphibia in the British Isles, with notes on Species recently introduced. *British Journal of Herpetology*, 1, 1-38.

Taylor, R.H.R. 1963. The Distribution of Amphibians and Reptiles in England and Wales, Scotland and Ireland and the Channel Islands: a Revised Survey. *British Journal of Herpetology*, 3, (5), 95-115.

Thorpe, R.S. 1979. Multivariate analysis of the population systematics of the ringed snake, *Natrix natrix* (L.). *Proceedings of the Royal Society of Edinburgh*, 78B, 1-62.

Thorpe, R.S. 1984. Geographic variation in the Western grass snake (*Natrix natrix helvetica*) in relation to hypothesized phylogeny and conventional subspecies. *Journal of Zoology, London*, 203, 345-355.

Tooley, M.J. 1990. The chronology of coastal dune development in the United Kingdom. In: Bakker, Th.W., Jungerius, P.D. and Klijn, J.A. (eds.). *Dunes of the European Coasts*. Catena Supplement, 18, 81-88.

Trueb, L. 1973. Bones, frogs, and evolution. In: Vial, J.L. (ed.). *Evolutionary Biology of the Anurans: Contemporary Research on Majore Problems*. University of Missouri Press, Columbia, 65-132.

Turner, A. 1981. Ipswichian mammal faunas, cave deposits and hyaena activity. *Quaternary Newsletter,* 33, 17-22.

Turner, C. 1996. A brief survey of the early Middle Pleistocene in Europe. In: Turner, C. (ed.) *The Early Middle Pleistocene in Europe*. A.A. Balkema, Rotterdam, 295-317.

Veith, M. 1997. *Salamandra salamandra* (Linnaeus, 1758). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe*. Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 68-69.

Vergnaud-Grazzini, C. 1966. Les amphibiens du Miocene de Beni-Mellal. *Notes Service. géolog. Maroc, Rabat*, 27, 43-74.

Vergnaud-Grazzini, C. 1970. Les amphibiens fossiles du gisement D'Arondelli. *Palaeont. Ital.*, 66, 47-65.

Waldén, H.W. 1955. Ett inlägg i diskussionen om relikt ätlig groda, *Rana esculaenta* i Mellansverige. *Sveriges Faun. Revy*, 4, 115-123.

Wallén, C.C. (ed.) 1970. *World Survey of Climatology Volume 5: Climates of Northern and Western Europe*. Elsevier Publishing Company, London.

Walker, M.J.C., Bohncke, S.J.P., Coope, G.R., O'Connell, M., Usinger, H. and Verbruggen,

C. 1994. The Devensian Weichselian Late-Glacial in Northwest Europe (Ireland, Britain, North Belgium, The Netherlands, Northwest Germany). *Journal of Quaternary Science,* 9, 109-118.

Walkling, A.P. 1996. *Coleopteran records from the Last Interglacial-Glacial transition.* Unpublished PhD thesis, Royal Holloway, University of London.

Walters, G.J. 1981a. Historical Aspects of British Herpetofauna Distribution. *British Journal of Herpetology*, 6, 177.

Walters, G.J. 1981b. Historical Aspects of British Herpetofauna Distribution: a reply. *British Journal of Herpetology*, 6, 178-179.

West, R.G. 1956. The Quaternary deposits at Hoxne, Suffolk. *Philosophical Transactions of the Royal Society of London*, B239, 263-356.

West, R.G. 1980. Pleistocene forest history in East Anglia. *New Phytologist*, 85, 571-622.

West, R.G. 1996. Outline of the stratigraphy and vegetational history of the Cromer Forest-bed Formation. In: Turner, C. (ed.) *The Early Middle Pleistocene in Europe.* A.A. Balkema, Rotterdam, 1-8.

West, R.G. and Sparks, B.W. 1960. Coastal interglacial deposits of the English Channel. *Philosophical Transactions of the Royal Society of London*, B243, 95-133.

Wilkinson, D.M. 1988. The Flandrian history of rare herptiles in Britain: a consideration of the hypotheses of Beebee and Yalden. *British Herpetological Society Bulletin*, 25, 39-41.

Wingfield, R.T.R. 1995. A model of sea-levels in the Irish and Celtic seas during the end-Pleistocene to Holocene transition. In: Preece, R.C. (ed.) *Island Britain: a Quaternary perspective*, Geological Society Special Publication No. 96, London, 181-208.

Wilson, J.P.F. 1983. The Postglacial colonisation of Ireland by fish, amphibians and reptiles. In: Sleeman, D.P., Devoy, R.J. and Woodman, P.C. 1983 (eds.). Proceedings of The Postglacial Colonisation Conference, University College, Cork, 15-16 October 1983. *Occasional Publication of the Irish Biogeographical Society,* 1.

Wolley, J. 1859. Is the Edible Frog a true Native of Britain? *Zoologist*, 17, 6606-6609.

Wymer, J. 1985. *The Palaeolithic sites of East Anglia.* Geo Books, Norwich.

Yalden, D.W. 1980. An alternative explanation of the distributions of the rare herptiles in Britain. *British Journal of Herpetology*, 6, 37-40.

Yalden, D.W. 1981. Historical Aspects of the British Herpetofauna Distribution: a reply. *British Journal of Herpetology*, 6, 178.

Yalden, D.W. 1982. when did the mammal fauna of the British Isles arrive? *Mammal Review*, 12 (1), 1-57.

Yu, G. and Harrison, S.P. 1995. Holocene changes in atmospheric circulation patterns as shown by lake status changes in northern Europe. *Boreas*, 24, 260-268.

Zagwijn, W.H. 1996. The Cromerian Complex Stage of the Netherlands and correlation with other areas in Europe. In: Turner, C. (ed.) *The Early Middle Pleistocene in Europe.* A.A. Balkema, Rotterdam, 145-172.

Zittel, K.A. 1887-90. *Handbüch der Palaeontologie. Volume 1: Palaeozoologie. Part 3: Vertebrata (Pisces, Amphibia, Reptilia, Aves).* R. Oldenbourg, Munich and Leipzig.

Zuiderwijk, A. 1997a. *Triturus marmoratus* (Latreille, 1800). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 82-83.

Zuiderwijk, A. 1997b. *Triturus alpestris* (Laurenti, 1768). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 72-73.

Zuiderwijk, A. 1997c. *Triturus helveticus* (Razoumowsky, 1789). In: Gasc *et al* (eds.) *Atlas of Amphibians and Reptiles in Europe.* Societas Europaea Herpetologica, and Museum National d'Histoire Naturelle, Paris, 78-79.

Appendix 1 - Inventory of skeletal specimens prepared

The following specimens have been prepared by the methods described in Chapter 4. For the salamandrids, lizards and snakes, lengths are measured from the snout to the tip of the tail (i.e total length). For the anurans, lengths are measured from snout to vent. Carapace lengths are given for *E. orbicularis*. Where information is not known, this is denoted by '-'. Some specimens of the non-British native species were captive-bred, but their ancestors would have been imported from mainland Europe originally.

***Salamandra salamandra* fire salamander**

Ref. No.	Sex	Length (mm)	Provenance
CGO 11/1	F	150	-

***Triturus marmoratus* marbled newt**

Ref. No.	Sex	Length (mm)	Provenance
CGO 23/1	-	-	-

***Triturus cristatus* great crested newt**

Ref. No.	Sex	Length (mm)	Provenance
CGO 6/1	M	120	-
CGO 6/2	F	-	-
CGO 6/4	-	c.140	E. Anglia
CGO 6/5	-	c.80	E. Anglia

***Triturus alpestris* alpine newt**

Ref. No.	Sex	Length (mm)	Provenance
CGO 9/1	F	91	-

***Triturus vulgaris* smooth newt**

Ref. No.	Sex	Length (mm)	Provenance
CGO 7/1	F	-	-
CGO 7/2	F	-	-
CGO 7/3	M	-	-
CGO 7/4	M	c.75	-
CGO 7/5	M	-	Kent

***Triturus helveticus* palmate newt**

Ref. No.	Sex	Length (mm)	Provenance
CGO 21/1	F	-	-

CGO 21/2	M	-	Canterbury, Kent
CGO 21/3	M	-	Canterbury, Kent
CGO 21/7	F	79	Coch y Dwst, Powys
CGO 21/8	F	81	Canterbury, Kent

***Bufo bufo* common toad**

Ref. No.	Sex	Length (mm)	Provenance
CGO 1/1	-	33	Eynsham, Oxon.
CGO 1/2	F	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/3	F	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/4	F	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/5	M	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/6	M	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/7	M	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/8	M	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/9	M	-	Loch Eadar da Bhaile, Raasay, Highland Region
CGO 1/10	M	-	Oskaig, Raasay, Highland Region
CGO 1/11	M	-	Oskaig, Raasay, Highland Region
CGO 1/12	M	-	Oskaig, Raasay, Highland Region
CGO 1/13	M	-	Oskaig, Raasay, Highland Region
CGO 1/14	M?	65	Sefton Coast, Merseyside
CGO 1/15	M	52	Doncaster, South Yorkshire
CGO 1/16	-	-	Deal, Kent
CGO 1/17	-	-	Deal, Kent
CGO 1/18	F	70	Cassington, Oxfordshire
CGO 1/19	-	-	Clipstone, Nottinghamshire
CGO 1/20	F	59	Idlecote, Warwickshire

***Bufo calamita* natterjack toad**

Ref. No.	Sex	Length (mm)	Provenance
CGO 17/1	M	59	Sefton Coast, Merseyside
CGO 17/2	M	-	-
CGO 17/3	F	-	-
CGO 17/4	-	-	-
CGO 17/5	-	-	-
CGO 17/6	M	76	Saltflatby Theddlethorpe, Lincolnshire
CGO 17/7	F	61	Cumbria
CGO 17/8	F	54	-

CGO 17/9	M	38	-

***Bufo viridis* green toad**

Ref. No.	Sex	Length (mm)	Provenance
CGO 29/1	M	67	-

***Rana temporaria* common frog**

Ref. No.	Sex	Length (mm)	Provenance
CGO 2/1	F	85	Allesley Park, Coventry, West Midlands
CGO 2/2	M	79	Vicar Water, Clipstone, Nottinghamshire
CGO 2/3	F	83	Vicar Water, Clipstone, Nottinghamshire
CGO 2/4	F	92	Gulson Road, Coventry, West Midlands
CGO 2/5	F	-	Warwick University, Coventry, West Midlands
CGO 2/7	F	69	?South Yorkshire
CGO 2/14	-	65	Birchington, Kent.
CGO 2/19	M	63	Canterbury, Kent
CGO 2/21	F	58	Canterbury, Kent
CGO 2/23	M	60	Canterbury, Kent
CGO 2/29	-	39	Acorns Hill, Dundee, Tayside
CGO 2/30	-	30	Acorns Hill, Dundee, Tayside

***Rana arvalis* moor frog**

Ref. No.	Sex	Length (mm)	Provenance
(C. Snell coll.)	-	-(Juv.)	-
(C. Snell coll.)	-	-	-
(C. Snell coll.)	M	42	Sweden
(C. Snell coll.)	F	60	Sweden

***Rana ridibunda* marsh frog**

Ref. No.	Sex	Length (mm)	Provenance
CGO 42/1	M	77	Isle of Grain, Kent
CGO 42/2	M	62	Bonington, Romney Marsh, Kent
CGO 42/3	M	70	Bonington, Romney Marsh, Kent
CGO 42/4	M	74	Bonington, Romney Marsh, Kent
CGO 42/5	M	30	Bonington, Romney Marsh, Kent
CGO 42/6	F	90	Bonington, Romney Marsh, Kent
CGO 42/7	F	83	Bonington, Romney Marsh, Kent
CGO 42/8	F	72	Bonington, Romney Marsh, Kent

CGO 42/9	F	57	Bonington, Romney Marsh, Kent
CGO 42/10	F	94	Bonington, Romney Marsh, Kent
CGO 42/11	F	56	Bonington, Romney Marsh, Kent
CGO 42/12	F	66	Bonington, Romney Marsh, Kent
CGO 42/13	F	71	Bonington, Romney Marsh, Kent
CGO 42/14	M	79	Isle of Grain, Kent
CGO 42/15	M	80	Isle of Grain, Kent
CGO 42/16	M	81	Isle of Grain, Kent
CGO 42/17	M	71	Isle of Grain, Kent
CGO 42/18	M	73	Isle of Grain, Kent
CGO 42/19	M	78	Isle of Grain, Kent

(These are from populations which are known to be introduced)

***Rana lessonae* pool frog**

Ref. No.	Sex	Length (mm)	Provenance
(J. Buckley coll.)		M -	Thompson Common, Norfolk
(C. Snell coll.)	-	-	Sweden
(C. Snell coll.)	-	-	Southeast London (?introduced)

***Rana esculenta* edible frog**

Ref. No.	Sex	Length (mm)	Provenance
CGO 44/1	F	56	Newdigate nursery, Surrey
CGO 44/2	M	67	Newdigate nursery, Surrey
CGO 44/3	F	76	Newdigate nursery, Surrey
CGO 44/4	F	75	Newdigate nursery, Surrey
CGO 44/5	F	72	Newdigate nursery, Surrey
CGO 44/6	F	78	Newdigate nursery, Surrey
CGO 44/7	F	76	Newdigate nursery, Surrey
CGO 44/8	F	74	Newdigate nursery, Surrey
CGO 44/9	F	64	Newdigate nursery, Surrey
CGO 44/10	M	52	Newdigate nursery, Surrey
CGO 44/11	F	45	Newdigate nursery, Surrey
CGO 44/12	F	48	Newdigate nursery, Surrey
CGO 44/13	M	46	Newdigate nursery, Surrey
CGO 44/14	M	44	Newdigate nursery, Surrey
CGO 44/15	-	37	Newdigate nursery, Surrey
CGO 44/16	-	24	Newdigate nursery, Surrey
CGO 44/17	-	22	Newdigate nursery, Surrey

CGO 44/18	-	19	Newdigate nursery, Surrey
CGO 44/19	-	20	Newdigate nursery, Surrey
CGO 44/20	-	19	Newdigate nursery, Surrey

(These are bred from specimens introduced from France)

***Emys orbicularis* European pond terrapin**

Ref. No.	Sex	Length (mm)	Provenance
CGO 30/1	M	130	-
CGO 30/2	-	140	-
CGO 30/3	-	137	-

***Lacerta agilis* sand lizard**

Ref. No.	Sex	Length (mm)	Provenance
CGO 18/1	M	182	Birkdale Dunes, Sefton Coast, Merseyside

***Lacerta vivipara* common lizard**

Ref. No.	Sex	Length (mm)	Provenance
CGO 41/1	M	146	Surrey

***Podarcis muralis* wall lizard**

Ref. No.	Sex	Length (mm)	Provenance
CGO 45/1	-	140	La Rochelle, France

***Anguis fragilis* slow-worm**

Ref. No.	Sex	Length (mm)	Provenance
CGO 16/1	-	155	Wickhambreaux, Canterbury, Kent
CGO 16/2	-	102	Canterbury, Kent
CGO 16/3	F	c.250	Canterbury, Kent
CGO 16/4	-	c.300	Canterbury, Kent
CGO 16/5	M	341	Plymouth, Devon

***Natrix natrix* grass snake**

Ref. No.	Sex	Length (mm)	Provenance
CGO 13/1	?F	815	York area, North Yorkshire
CGO 13/2	-	-	Nr. Abbots Morton, Warwickshire
CGO 13/4	-	826	Doncaster, South Yorkshire

Natrix maura **viperine snake**

Ref. No.	Sex	Length (mm)	Provenance
CGO 3/1	-	255	-

Coronella austriaca **smooth snake**

Ref. No.	Sex	Length (mm)	Provenance
CGO 28/1	-	665	-

Vipera berus **adder**

Ref. No.	Sex	Length (mm)	Provenance
CGO 20/1	F	460	Helton, Carlisle, Cumbria

Coronella austriaca **smooth snake**

Ref. No.	Sex	Length (mm)	Provenance
CGO 28/1	-	665	-

Vipera berus **adder**

Ref. No.	Sex	Length (mm)	Provenance
CGO 20/1	F	460	Helton, Carlisle, Cumbria